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EVOLUTIONARY STUDIES ON THE DISTRIBUTION AND DYNAMICS OF MELANISM IN THE HAMSTER (CRICETUS CRICETUS L.). I. DISTRIBUTION OF BLACK HAMSTERS IN THE UKRAINIAN AND BASHKIRIAN SOVIET SOCIALIST REPUBLICS (U.S.S.R.)[1]

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THE PROBLEM of natural selection is one of the most important and, at the same time, least investigated in evolutionary biology. It has been treated chiefly through rather elaborate mathematical calculations based on *a priori* assumptions, since actual observations have been scarce and the data obtained meagre. The most promising method for investigating the laws of natural selection is detailed study of changes which take place in wild populations of a species in the course of several generations. Of course, changes in the frequencies of different types of individuals in a population may depend not only on natural selection but on other factors as well, such as chance survival, migration, etc. Where the biology of the organisms concerned is insufficiently known, it may be difficult to evaluate the part played by natural selection in the complex of factors which influence the structure and composition of the populations. On the other hand, there remains the possibility of tracing the actual mechanisms of the transformation of wild populations by natural selection and of discovering the paths by which new races and varieties are created.

The common hamster (*Cricetus cricetus* L.) provides favorable material for studies of this kind. Its natural populations often contain considerable proportions of melanic individuals—that is, they are dimorphic with respect to an easily classifiable trait. Such differences in coat color in rodents are hereditary and are highly independent in their expression from environmental modification. As shown by GERSHENSON and POLEVOI (1940, 1941) and GERSHENSON (1941), the black coat color in the hamster is inherited as a simple autosomal dominant, and the matings between black and normal hamsters occur in wild populations at random. Different populations contain diverse proportions of melanic individuals. As with most rodents, the hamster breeds rapidly, and its biology is well known. These rodents are the object of a fairly developed branch of fur trade. Data concerning the proportions of black and normal hamsters trapped during a number of years by several factories of "Soiuspushnina" (All-Union Fur Syndicate) located in two different geographical zones of the European part of U.S.S.R., in the Ukraine and in Bashkiria were made available for the study reported here. This provided far more material

[1] Manuscript of this and the following paper by Dr. S. GERSHENSON were received through the Science Committee of the National Council of American-Soviet Friendship. They were edited and prepared for publication by TH. DOBZHANSKY.

than could be obtained through field collections alone. Since in the hamster the generations overlap, and since the duration of the reproductive period is not exactly known, the calculations necessary to determine the intensity of natural selection are necessarily complicated.

Extraction of the pertinent data from the archives of "Soiuspushnina" was a laborious process which required careful examination of many thousands of records of local factories. The author wishes to acknowledge obligation in the fulfillment of this task to I. GRUSHEVSKAIA, M. ILCHENKO, and I. LITOSHENKO.

LITERATURE REVIEW

The existence of black hamsters has been known for a long time. As early as 1769, PALLAS (1771) observed considerable numbers of them near Simbirsk (now Ulianovsk), and later (PALLAS 1778) he reported their presence in other localities of the Volga region, especially near Kazan, and in the Ural region, especially near Ufa. LEPEKHIN (1771) likewise found black hamsters near Simbirsk and in the former Ufa province during his journey in 1768–69. GEORGI (1775) pointed out that in 1772 black hamsters were frequent near Kazan where their pelts were extensively used in the fur industry. About the same time SULZER (1774) and BECHSTEIN (1789, 1807) found them in the western part of the species area in Thuringia, Germany.

In the nineteenth century, LÜBEN (1848) mentioned the existence of black hamsters in Saxony, EVERSMANN (1850) along the rivers Belaia, Kama, Volga, and throughout the Kazan province, where they are more frequent than normal ones, and KESSLER (1851) near Zolotonosha (in the vicinity of Poltava). According to BOGDANOV (1871), only black hamsters are to be found in the northern part of the former Kazan province, while in the southwestern part, as well as in the former Saratov and Simbirsk provinces, exclusively normally colored hamsters occur. KARELIN (1875) recorded black hamsters in the Ural region.

Much information about black hamsters has appeared since the beginning of the present century. According to KRULIKOVSKY (1902), exclusively black hamsters are found in the former Viatka province, but according to SCHITKOFF (1905), they are rather rare in the former Simbirsk province but very frequent near Kazan, where they completely supplant in some places the normal ones. SIMROTH (1905, 1906) presented data on black hamsters in Thuringia, BYKOVSKY (1913) and STACH (1920) in the neighborhood of Tarnopol, KRYZHOV (1935) near Dniepropetrovsk, and JAKOBI (1928) re-examined the black hamster situation in Thuringia. KRYSHTAL (1929) gave detailed information about black hamsters collected near Berdichev; PIDOPLICHKA (1928, 1930a) reported their occurrence in the part of the Ukraine west of the Dnieper, ARGIROPULO (1931) near Kurgan, NOVIKOV (1932) found them in the Caucasus and near Gomel, KUZNETSOV (1932) in Tataria and Bashkiria, KUNTZE and SZYNAL (1933) in different localities of the western Ukraine, and KIRIKOV (1934) in different districts of Bashkiria and near Gorky and Rostov-on-Don. DIAKONOV and SULLA (1935) also reported on frequency of black hamsters in Bashkiria.

PETZSCH (1936) in a monograph on the biology of reproduction of the hamster included detailed data on the distribution of the black coat color in Germany. MIGULIN (1938) in a review of Ukrainian mammals stated that black hamsters exist near Kharkov and that apparently their distribution in the Ukraine is much wider than is indicated in the literature. Papers by TIMOFEEFF-RESSOVSKY (1939a, 1939b) attempt to give a picture of the distribution and dynamics of black hamsters during the last 150 years.

Some authors have attempted to define the ecological conditions under which black hamsters are especially frequent. Thus, it was SCHITKOFF's (1905) opinion that they are found predominantly on clay soil covered with oak or mixed forests. SIMROTH (1906) connected their appearance in Thuringia with an exceptionally hot summer. HILZHEIMER (1913) suggested that in the Volga region they are most frequent in moist places, and KIRIKOV (1934) regarded them as chiefly a forest and river bank form. According to PETZSCH (1936), black hamsters increase in frequency in years when the total numbers of hamsters are great and decrease in years when hamsters are scarce. TIMOFEEFF-RESSOVSKY (1939a) observed that black hamsters are especially frequent in the cool and humid climate near the northern border of the distribution area of the species.

Descriptions of the melanic hamsters given by various authors coincide with one another fairly well. In all cases it is stated that melanic hamsters are totally black, with the exception of feet, tail, nose, upper lip, and margins of the ears, which are covered with white hair; in some cases white spots are present on the throat and chest. According to STACH (1920), black hamsters from the vicinity of Tarnopol have white margins of the ears and white feet; the rest of the body is black, but behind the ears and near the tail a reddish tinge is discernible. A detailed examination shows that each hair is not self-colored but gray at base, reddish in the middle, and black near the tip. This is especially clearly seen on the back and near the tail. Some individuals have white hairs on the upper lip; sometimes one or two longitudinal reddish stripes are present on the back. Besides these typical melanics, a much rarer type characterized by the presence of large irregular white spots has been reported (PALLAS (1789) and KIRILOV (1934) from the Ural region, BECHSTEIN (1789, 1807) in Thuringia). Such spotted black hamsters occur only in localities in which the usual melanics occur also. BOGDANOV (1871) and PETZSCH (1936) have observed that black hamsters are somewhat larger than normally colored ones, but other authors (for example, KESSLER 1851) have found no such size difference.

The taxonomic rank of black hamsters has been evaluated differently by different authors. PALLAS (1778) pointed out that they do not form a separate species, since they mate with normal ones and are often found together with the latter in the same litters. LEPEKHIN (1771) also ranked them as a variety but thought that they breed true. SCHREBER (1792) was first to regard black hamsters a subspecies, and TROUESSART (1910) gave them the name *Cricetus cricetus niger* Schreb. SIMROTH (1906) called them a mutation, STACH (1920) a "morpha," KIRIKOV (1934) defined them essentially as an ecotype.

The inheritance of the black coat color attracted the attention of several investigators. FISCHER (1874) attempted to solve this question experimentally, but his description of the crosses is so confused that no conclusions can be drawn. KRYSHTAL (1929) and PETSZCH (1936) examined ten or fewer litters of hamsters collected in nature and concluded that the black coloration is due to a recessive gene. Reinvestigation of this problem by GERSHENSON and POLEVOI (1940, 1941) on incomparably greater material definitely showed that melanism in the hamster is due to a simple autosomal dominant, probably homologous to the gene E^D for dominant black coloration known in the rabbit and in the black rat.

MATERIAL AND METHODS

The present work is based on the records of hamster pelts purchased by the local factories of "Soiuspushnina" in different districts of Ukraine in 1934–1939 (about two millions) and on field collections by the author made in 1939–1941. The data for Bashkiria come from records of 49 districts of "Soiuspushnina" and embrace more than one million hamsters trapped in the summer of 1933 and during the years 1937–1939.

In all, data of 529 district factories in the Ukraine covering about 445,000 square kilometers were available. The average territory covered by a factory is about 840 square kilometers, but the factories are not distributed evenly. Moreover, factories located in larger settlements, railway stations, and river ports may possibly obtain pelts from greater territories than factories in small and distant villages. The records of the district factories give the numbers of pelts purchased each month, the normal and the black pelts being recorded separately, since the latter are purchased at a higher price than the former. The district factories in Bashkiria cover a territory of about 140,000 square kilometers. The average territory covere dby a factory is here about 2,800 square kilometers, or more than three times larger than in the Ukraine, but the factories are distributed unevenly, being more numerous in the western and central than in the sparsely populated eastern part of the country.

It is important to examine the possible sources of errors in the records of "Soiuspushnina" factories with respect to the numbers of normal and black hamsters found in the different districts. Hamster pelts differ so clearly from those of other species of mammals, and the population is so well acquainted with hamsters, that misclassification of the species is very unlikely; examination of extensive material in the storehouses of "Soiuspushnina" revealed no instances of misclassification. Pelts of normal and of black hamsters are so sharply different from each other that mistakes in classification are excluded. Only in Bashkiria a slight error in classification is possible. As shown by KIRIKOV (1934), in some districts of Bashkiria, chiefly in the north, some of the black hamsters have white spots. At the fur factories most of these spotted blacks (those in which white hairs cover less than a quarter of the body surface) are classified as "Black," whereas a small minority in which the white spots are more extensive than one-quarter of the body are counted among the "Normals." As a result, the records of "Soiuspushnina" in Bashkiria may show

a slightly reduced frequency of the melanics. Hamsters are caught either by digging them out, by flooding their holes with water, or by setting traps at the entrance of the holes. No selection with respect to the coat color can occur. The hunting population does no use hamster pelts for its own needs and sells all the pelts to "Soiuspushnina."

As shown below, the frequency of black hamste s may vary greatly from district to district in the same region and also between localities within a district. Since trappers may be more active in some parts of a district than in others, the records of "Soiuspushnina" may not show the true frequencies of the black and normal hamsters within the district. This distortion, however, is not very serious; the number of trappers in each district is usually several dozen, and their hunting territories overlap each other so that the chance variations in the activities of the individual trappers are levelled off in the total. The records of the "Soiuspushnina" factories reflect, therefore, the actual

TABLE 1

Comparison of the frequencies of black hamsters observed during field work and those indicated by the records of "Soiuspushnina."

DISTRICT	TOTAL EXAMINED	NUMBER OF BLACK	PERCENTAGE BLACK
Malo-Devitsa, "Soiuspushnina"	6798	1781	26.2±0.5
Malo-Devitsa, Author's observations	694	172	24.8±1.6
Novo-Bassan, "Soiuspushnina"	585	23	3.9±0.8
Novo-Bassan, Author's observations	118	4	3.4±1.7

frequencies of the normal and black hamsters in the respective districts with a reasonable accuracy. This conclusion is confirmed by checking the records of "Soiuspushnina" in some districts against the results of observations made by the author during field work in the Malo-Devitsa district of the Chernigov region in July and August of 1939, and in the Novo-Bassan district of the same region in September of 1940 (table 1). The agreement between the data of "Soiuspushnina" and those of the author is very good.

DISTRIBUTION OF BLACK HAMSTERS IN THE UKRAINIAN S.S.R.

A summary of the data concerning the total number of hamsters and the number of black hamsters trapped in 1934–1939 in different regions of the Ukrainian S.S.R. is given in table 2. Data from 529 district factories, were available for the study, but the records of only 386 of those which had purchased more than 100 pelts during the respective years were used.

The frequencies of black hamsters differ not only in different regions of the Ukrainian S.S.R. but also in different districts within a region. Within a district, however, the frequency of black hamsters is relatively constant from year to year. This can be seen by plotting the data for the different years on maps and comparing the maps. A more precise method is to determine the correla-

TABLE 2

Number of normal and black hamsters trapped in different regions of the Ukrainian S.S.R. during 1934–1939.

REGIONS	1934			1935			1936			1937			1938			1939			TOTAL		
	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK	TOTAL	BLACK	PERCENTAGE OF BLACK
1. Vinnitsa	No data			38,508	16	0.04	44,250	502	1.13	2,506	31	0.12	33,436	646	1.93	14,331	488	3.41	155,586	1,683	1.08
2. Voroshilovgrad	3,114	1	0.03	1,114	0	0.00	764	1	0.13	1,508	1	0.06	1,320	0	0.00	No data			7,820	3	0.04
3. Dniepropetrovsk	32,551	45	0.14	12,480	62	0.50	26,521	29	0.11	30,127	19	0.63	16,769	93	0.55	No data			118,448	248	0.21
4. Zhitomir	No data			9,349	42	0.45	28,807	1,159	4.02	16,903	533	3.15	14,882	347	2.33	13,055	499	3.82	82,996	2,580	3.11
5. Zaporozhie	4,429	1	0.02	2,387	0	0.00	3,673	0	0.00	3,500	0	0.00	3,005	0	0.00	1,086	0	0.00	18,079	1	0.01
6. Kamenets-Podolsk	No data			17,229	249	1.45	99,614	4,239	4.26	90,883	4,069	4.48	67,608	3,948	5.84	57,668	3,635	6.30	333,002	16,140	4.85
7. Kiev	No data			45,912	329	0.72	23,307	288	1.24	28,367	475	1.67	45,290	930	2.05	45,251	1,158	2.56	188,127	3,180	1.69
8. Kirovograd	17,063	1	0.01	10,112	4	0.04	13,822	3	0.02	18,997	3	0.02	15,634	16	0.10	6,648	8	0.12	82,276	35	0.04
9. Nikolaev	No data			2,134	0	0.00	4,692	0	0.00	4,741	47	0.99	3,189	0	0.00	2,306	0	0.00	17,062	47	0.27
10. Odessa	No data			3,494	7	0.20	7,841	38	0.48	5,841	34	0.58	16,066	285	1.77	6,458	107	1.66	39,700	471	1.12
11. Poltava	21,277	2,326	10.93	20,603	3,158	15.33	30,446	2,616	8.59	48,262	3,218	6.67	47,260	2,438	5.16	No data			167,848	13,756	8.20
12. Stalino	13,932	765	5.49	5,182	173	3.33	9,787	55	0.56	8,235	218	2.65	4,685	0	0.00	No data			41,821	1,211	2.90
13. Sumy	3,726	39	1.05	20,110	25	0.12	16,170	113	0.70	26,304	247	0.87	29,061	74	0.25	No data			97,371	498	0.51
14. Kharkov	5,120	34	0.66	3,897	88	2.26	5,862	188	3.21	11,596	416	3.59	6,481	177	2.73	No data			32,956	903	2.74
15. Chernigov	No data			73,018	1,300	1.78	78,610	2,508	3.19	93,586	1,962	2.10	173,708	5,398	3.11	163,611	8,645	5.28	582,533	19,813	3.40
Grand total	101,212	3,212	3.17	265,529	5,453	2.05	394,166	11,739	2.80	415,911	11,273	2.71	478,393	14,353	3.00	310,414	14,540	4.68	1,965,625	60,570	3.08

tion coefficients between the frequencies of black hamsters within a district in different years. The correlation coefficient for successive years calculated from the data of 386 district factories is $+0.66 \pm 0.02$. The average frequencies of black hamsters during the entire period for which data are available are therefore satisfactory characteristics of the respective districts. A considera-

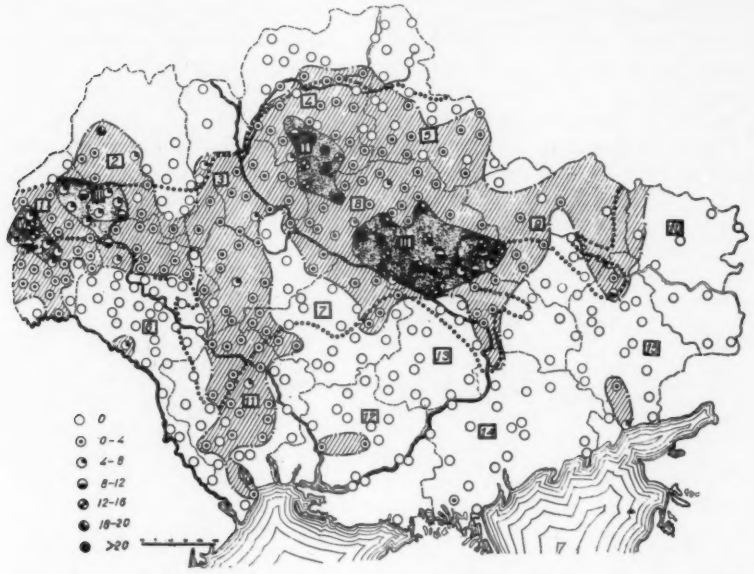

FIGURE 1. Distribution of black hamsters in the Ukrainian S.S.R. in 1934–1939. Stippled area—the distribution of melanics. I, II, III, IV—zones of high frequency of melanics. 1—Kamenets-Podolsk region; 2—Zhitomir region; 3—Kiev region; 4—Chernigov region; 5—Sumy region; 6—Vinnitsa region; 7—Kirovograd region; 8—Poltava region; 9—Kharkov region; 10—Voroshilovgrad region; 11—Odessa region; 12—Nikolaev region; 13—Dniepropetrovsk region; 14—Zaporozhie region; 15—Stalino region. Dotted line—boundaries of the forest-steppe zone. Circles—frequency of melanics in percentage. Scale in kilometers.

tion of changes in the frequencies from year to year is given in the following paper.

The map of the Ukraine in figure 1 shows the boundaries of the territory in which black hamsters were recorded in 1934–1939. The data of all factories, regardless of the numbers of hamster pelts they purchased, are included in this map provided any black hamsters were encountered among them. It may be seen from the map that the main distribution area in the Ukraine is practically continuous. Aside from this main area, there exist five "islands" where black hamsters are found surrounded by districts where no blacks were observed during the period studied. The "island" at the southwestern boundary may in reality be connected with the main area. BYKOVSKY (1913), STACH

(1920), and KUNTZE and SZYNAL (1933) found black hamsters near Tarnopol, Lvov, and north of Stanislav. This is confirmed by unpublished observations of RESHETNIK who did some field work in that region in 1940, and also by some preliminary data obtained by the writer in 1940 from the fur factories in that region (in some localities near Lvov and Tarnopol up to 10 per cent of black hamsters are found in the populations). The other four "islands," however, are independent of the main area. In each of two of them, that are located in the Chernigov region and near Odessa, a single black hamster was trapped among approximately 40,000 and 1,200 normals respectively. The "islands" in the Nikolaev and Stalino regions are doubtless real, though the frequency of melanics is very low in both of them.

Figure 1 indicates that within the main area of distribution there exist four zones in which the frequencies of the melanics are especially high. These zones

TABLE 3

Frequencies of black hamsters within a 20 kilometers broad strip of land lying inside and a similar strip lying outside the boundaries of the zones of high frequencies of melanics.

ZONE	INSIDE 20 KILOMETERS STRIP			OUTSIDE 20 KILOMETERS STRIP		
	NUMBER OF POINTS	AVERAGE PERCENTAGE	RANGE OF PERCENTAGES	NUMBER OF POINTS	AVERAGE PERCENTAGE	RANGE OF PERCENTAGES
I	8	17.58	10.67–27.14	11	1.49	0.00–4.52
II	11	16.07	5.00–41.48	13	1.68	0.00–3.80
III	7	8.87	6.34–13.52	9	3.45	0.51–4.40
IV	8	7.46	5.31–10.45	10	1.95	0.00–4.85

are marked in figure 1 by Roman numerals I to IV. In each of the four zones the frequency of black hamsters exceeds 5 per cent and may reach 20 per cent and higher. The first zone is located in the southern part of Chernigov and the adjacent part of Poltava regions. The second lies in the southeastern part of the Poltava region. The third is in the western part of the Kamenets-Podolsk region, and probably extends westward into the territory not considered in the study. The fourth lies in the northeastern part of Kamenets-Podolsk, northwestern part of Vinnitsa, and southwestern part of Zhitomir regions.

It is interesting to note that the outlines of these zones are nearly everywhere very sharp. This is shown in figures 2 and 3 which give exact average frequencies of black hamsters within, and in the immediate vicinity of, the Chernigov and Poltava zones of high frequency of black hamsters. Table 3 summarizes the frequencies of black hamster within a 20 kilometer broad strip of territory lying inside and one lying immediately outside the boundaries of each of these four zones.

The data presented in figures 2 and 3 and in table 3 show that the percentages of black individuals take a sharp drop at the boundaries of the zones outlined above, the transition being accomplished within a distance not exceeding

40 kilometers and in many places (for example, at the northeastern boundary of the first zone and the northern and southwestern boundaries of the second zone) within 10–15 kilometers. Examination of the parts of the territory from which data are available from points located close to each other suggests that such sharp transitions are characteristic of all four zones. Cases are not infrequent where a point lying within a zone constantly shows very high percentages of black hamsters, and another point lying just outside the zone as con-

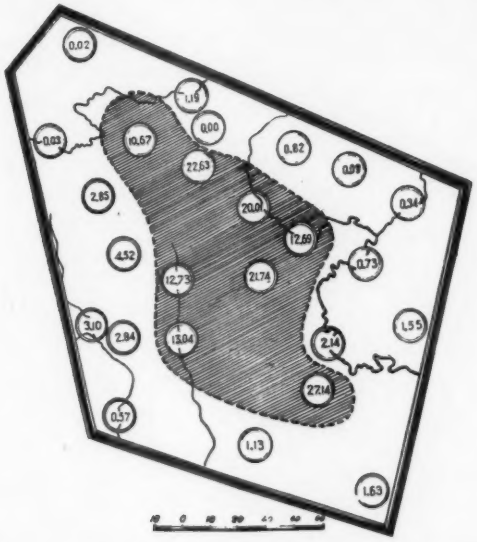

FIGURE 2. The Chernigov zone of high frequency of melanics. Circles—frequency of melanics in percentage. Scale in kilometers.

stantly shows very low percentages. The following examples may illustrate this. Losinovka and Talalaevka (first zone) are 12 kilometers apart and show 22.63 and zero per cent of melanics respectively; Grebenka (27.14 per cent) and Piriatin (2.14 per cent) in the first zone are 18 kilometers apart; Gradizhsk (22.05 per cent) and Novogeorgievsk (0.05 per cent) in the second zone are 15 kilometers apart; Felshtin (13.52 per cent) and Yarmolinzy (1.03 per cent) in the third zone are separated by only 9 kilometers.

Outside the four zones lie numerous districts with much lower frequencies of black hamsters. Such districts constitute a majority of all districts of the Ukraine in which melanics were recorded during the period investigated, and have usually one per cent of black hamsters or less. No classification of these districts on the basis of the frequencies of melanics in them can safely be made. Observation indicates that in the vicinity of the zones of high frequency of melanics (especially zones I and II) the percentage of black hamsters is some-

TABLE 4

Total number of hamsters and number of black hamsters trapped in 1933 and in 1937–1939 in different districts of the Bashkirian A.S.S.R.

DISTRICT	MAY–AUGUST 1933			1937			1938			1939			TOTAL FOR 1937–1939		
	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK	TOTAL	BLACK	PER-CENTAGE OF BLACK
1. Abzelilovo	103	0	0.00	2,610	0	0.00	2,976	0	0.00	932	0	0.00	6,518	0	0.00
2. Arkhangelskoie	4,631	1,508	34.50	9,148	4,434	48.47	7,705	3,918	50.85	3,030	1,421	46.90	19,883	9,773	49.15
3. Askino		No data		12,804	7,512	58.67	21,286	11,726	55.09	13,514	7,447	55.11	47,604	26,685	56.02
4. Aurgazy	1,033	156	15.10	712	145	20.36		No data			No data		712	145	20.36
5. Baikibashevo		No data			No data			No data		1,977	1,407	71.17	1,977	1,407	71.17
6. Baimak	1,423	0	0.00	1,272	0	0.00	1,113	0	0.00	3.32	0	0.00	2,717	0	0.00
7. Bakaly	989	38	3.84	1,104	29	2.63		No data			No data		1,104	29	2.63
8. Baltachevo	503	306	60.83	13,250	9,159	69.12	46,241	32,848	71.04	19,432	13,578	69.87	78,923	55,585	70.43
9. Belebei	314	0	0.00	52	1	1.92		No data			No data		52	1	1.92
10. Belokatai	1,567	278	17.74	8,328	1,103	13.24	16,506	1,794	10.87	14,685	1,787	12.17	39,519	4,684	11.85
11. Beloretsk	335	5	1.49	441	12	2.72	1,054	30	2.84	477	5	1.05	1,972	47	2.38
12. Birsk	12,617	5,843	46.31	12,417	8,954	72.11	22,301	16,096	71.98	14,955	10,360	69.27	49,733	35,410	71.20
13. Blagoveshchensk	786	511	65.01	5,802	4,351	74.99	12,816	9,774	76.26	8,210	5,937	72.31	26,828	20,062	74.78
14. Buraevo	1,485	1,048	70.57	18,116	14,670	80.98	38,280	28,632	74.80	13,858	10,503	75.79	70,254	53,805	76.59
15. Burzian	51	0	0.00	221	1	0.45	1,319	0	0.00		No data		1,540	1	0.06
16. Buzdiak	4,577	477	9.77		No data			No data			No data			No data	
17. Chekmagushevo	5,385	939	17.44		No data			No data			No data			No data	
18. Chishmy	405	37	9.14		No data			No data			No data			No data	
19. Davlekanovo	674	42	6.23		No data			No data			No data			No data	
20. Diurtiulli	5,286	1,021	19,32	2,236	1,097	49.06		No data		258	151	58.53	2,494	1,248	50.04
21. Duvan	3,244	447	13.78	187	25	13.37	5,868	703	11.98	4,426	319	7.21	10,481	1,047	9.99
22. Iglino	520	453	87.12	7,533	5,498	72.99	7,164	5,021	70.09	2,663	1,920	72.10	17,360	12,439	71.65
23. Kaltasy	2,685	1,259	46.89	8,343	5,442	65.23	26,874	18,140	67.50	7,248	4,799	66.21	42,465	28,381	66.83
24. Karaidel	3,091	1,698	54.93	7,559	5,019	66.40	19,468	12,419	63.79	8,330	5,205	62.48	35,357	22,643	64.04
25. Karmaskaly	791	222	28.07		No data			No data			No data			No data	
26. Khaibullino	1,218	0	0.00	1,600	0	0.00	419	0	0.00	738	0	0.00	2,757	0	0.00
27. Kizi	151	1	0.66		No data			No data			No data			No data	
28. Krasnokamsk		No data		9,250	3,668	41.82	23,478	10,641	45.32	11,812	4,916	41.62	44,540	19,425	43.61
29. Krasnousolsk	2,188	285	13.02	18,725	1,989	10.62	31,910	4,620	14.48	8,230	1,249	15.18	58,865	7,858	13.35
30. Kugarchi	146	0	0.00	3,611	0	0.00	12,518	0	0.00	8,703	0	0.00	24,832	0	0.00
31. Kushnarenkovo	1,053	203	19.28	467	153	32.76	1,839	551	29.96	2,201	503	22.85	4,507	1,207	26.78
32. Makarovo	2,828	28	0.99	12,161	365	3.00	32,268	737	2.28	10,001	193	1.93	54,430	1,295	2.38
33. Maloyaz		No data		4,002	49	1.25	10,621	223	2.10	8,298	161	1.94	22,921	433	1.89
34. Mechetlino	1,138	148	13.01		No data			No data			No data			No data	
35. Meleuz	904	0	0.00	11,841	14	0.12	18,956	182	0.96		No data		30,797	196	0.64
36. Mishkino	209	177	84.69	15,675	12,070	77.00	50,381	38,446	76.32	26,661	21,179	79.44	92,717	71,695	77.34
37. Miyakino	2,190	21	0.96	2,640	49	1.86	8,556	18	0.21	2,872	20	0.70	14,068	87	0.62
38. Nurimanovo	4,070	2,771	68.08	14,949	12,133	81.16	23,274	19,118	82.14	12,907	10,523	81.53	51,130	41,774	81.70
39. Sterlitamak	4,765	195	4.09	1,901	151	7.94	3,312	221	6.67	615	42	6.83	5,828	414	7.10
40. Tatyshly		No data		8,109	5,876	72.46	16,393	12,244	74.74	7,620	5,414	71.05	32,112	23,534	73.29
41. Tuimazy	1,732	48	2.77	365	2	0.55	5,046	9	0.18	3,450	11	0.35	8,861	22	0.25
42. Uchaly	39	0	0.00		No data			No data			No data			No data	
43. Ufa	2,410	1,080	44.81	7,161	2,289	31.96	10,222	4,260	41.67	2,507	791	31.55	19,890	7,340	36.90
44. Ulueliak		No data			No data			No data		76	59	77.63	76	59	77.63
45. Voskressensk		No data			No data			No data		594	6	1.01	594	6	1.01
46. Yanaul	6,309	4,574	72.50	19,137	13,836	72.30	29,283	21,996	75.12	11,167	7,859	70.38	59,587	43,691	73.32
47. Yumaguzino		No data		6,148	4	0.07	14,359	1	0.01	5,802	0	0.00	26,309	5	0.02
48. Zilair	5,109	1	0.02	1,129	0	0.00	9,530	0	0.00	10,660	0	0.00	21,319	0	0.00
49. Ziyanchurino	3,842	0	0.00	2,044	0	0.00	14,689	0	0.00	5,129	0	0.00	21,862	0	0.00
TOTAL	92,976	25,880	27.83	253,050	120,300	47.54	548,075	254,368	46.41	254,370	117,765	46.14	1,055,495	492,433	46.65

what higher than it is farther away, but this cannot be conclusively demonstrated.

DISTRIBUTION OF BLACK HAMSTERS IN THE BASHKIRIAN A.S.S.R.

Data on the total numbers of hamsters and the numbers of black hamsters trapped in different administrative districts of the Bashkirian A.S.S.R. during the summer of 1933 and the years 1937–1939 are summarized in table 4. In spite of the fact that different districts are characterized by very different frequencies of black hamsters, the frequency of melanics in each individual district remains fairly constant from year to year. The correlation coefficient

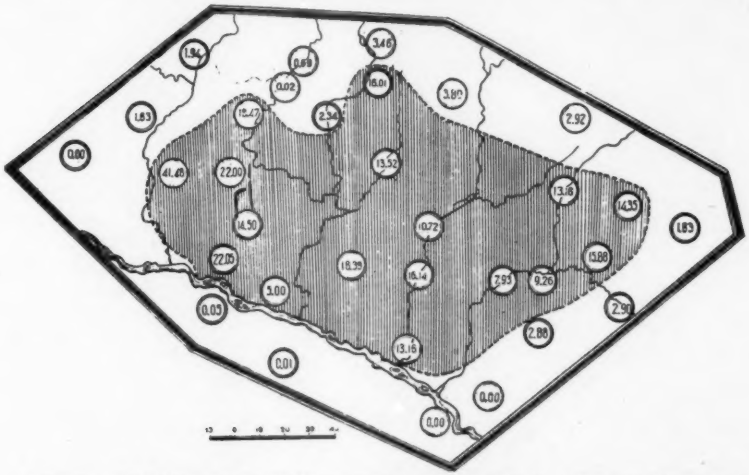

FIGURE 3. The Poltava zone of high frequency of melanics. Circles—frequency of melanics in percentage. Scale in kilometers.

between the frequencies of black hamsters in the same districts on successive years is $+0.99 \pm 0.04$. The constancy from year to year in Bashkiria, therefore, is even higher than it is in the Ukraine.

The geographic distribution of black hamsters in Bashkiria is shown in figure 4 on the basis of the average frequencies for 1937–1939 given in table 4. Black hamsters occur throughout Bashkiria with the exception of the southeastern part. The distribution area of the melanics is continuous, though their frequencies vary greatly in different localities within this area. The districts with over 60 per cent of black hamsters lie together, forming a compact zone. This zone is surrounded by a few districts with intermediate percentages (20–60 per cent), beyond which lie the districts with relatively low frequencies of melanics.

Aside from the data summarized in figure 4, data were also available concerning hamster pelts purchased by 41 district factories from May to August 1933; seven of these factories, located chiefly in western Bashkiria, are not repre-

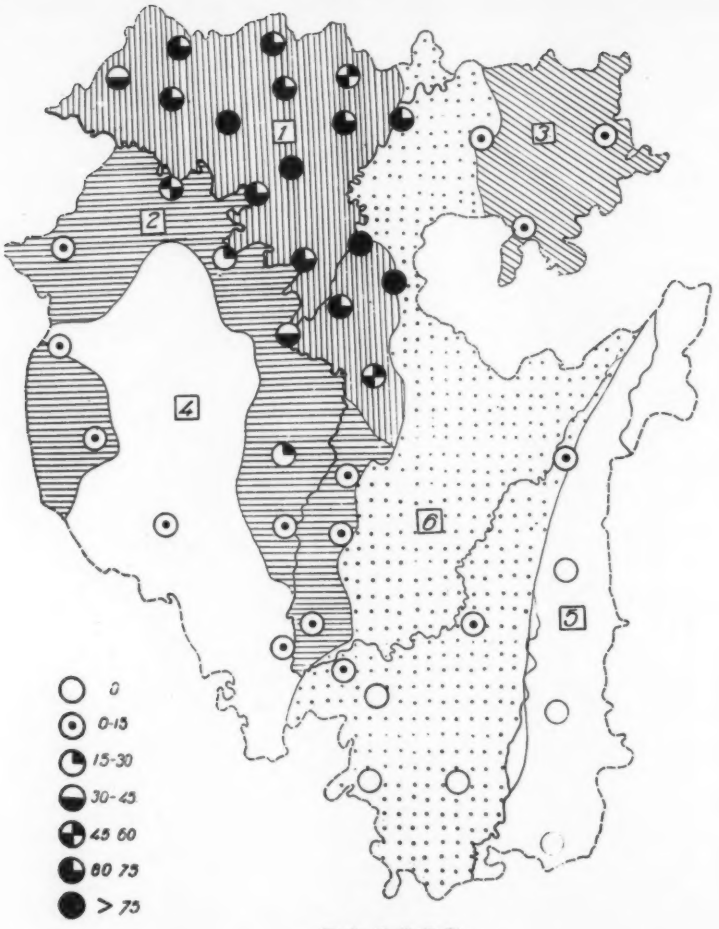

FIGURE 4. Distribution of black hamsters in the Bashkirian A.S.S.R. in 1937–1939. 1—humid forest-steppe region; 2—dry forest-steppe region; 3—mountain forest-steppe region; 4—Pre-Ural steppe region; 5—Trans-Ural steppe region; 6—mountain forest region. Circles—percentage of melanics. Scale in kilometers.

sented in the data for 1937–1939. Since, as shown in the following communication, the frequency of black hamsters is subject to some seasonal fluctuations, the data for 1933 collected during the summer months only are not fully comparable with the data for the years 1937–1939. However, the general features of the distribution of black hamsters can be ascertained even on the basis of data for a part of the year only. Figure 5 shows that all main features of the

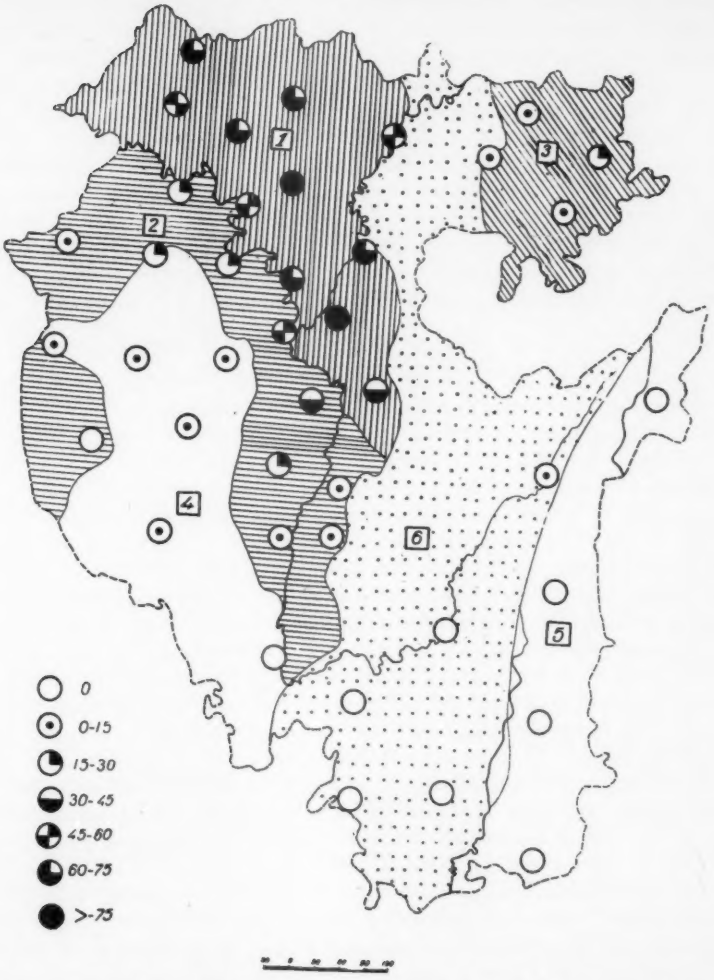

FIGURE 5. Distribution of black hamsters in the Bashkirian A.S.S.R. in the summer of 1933. Designations as in figure 4. Scale in kilometers.

distribution of black hamsters in 1933 coincide with what was observed in 1937–1939. It should be noted that these data are in good accord also with the more fragmentary information of KIRIKOV (1934) and DIAKONOV and SULLA (1935).

The types of distribution shown by black hamsters in Bashkiria and the Ukraine have much in common. In both areas black hamsters are met within

a large portion of the species distribution range, and the areas where the melanics occur are in the main continuous. The points where black individuals are particularly frequent are in both cases concentrated in discrete zones. The boundaries of these zones are generally well defined. Thus, between Karaidel and Duvan (60 kilometers) the frequency of black hamsters falls from 64 to 10 per cent, and between Iglino and Ufa from 70 to 37 per cent in less than 30 kilometers. The distribution of black hamsters in Bashkiria differs, however, from that in the Ukraine in two respects. First, the frequencies of the melanics are on the whole much higher in Bashkiria. Secondly, the zone of the high frequencies is surrounded in Bashkiria by several districts with intermediate frequencies of melanics, whereas in the Ukraine such gradients either do not exist or are but weakly pronounced.

CAUSES OF THE EXISTENCE OF BLACK HAMSTERS IN SOME PARTS OF THE UKRAINE AND THEIR ABSENCE IN OTHER PARTS

Black hamsters are present in some and absent in other parts of their distribution region in the Ukraine. This evidently cannot be explained by chance fluctuations in the reproduction and survival of the two types of hamsters, since in such a case the distribution of melanics over the vast territory where they are found could not be continuous. Three other possible explanations may be advanced. First, it can be supposed that the black mutation of the hamster, having arisen somewhere inside the investigated territory or having penetrated therein from the outside, is gradually spreading (diffusing) from its point of origin over the area of distribution of the species, but as yet has not had enough time to spread over the whole of it. Secondly, the limited distribution of melanism in only a part of the area occupied by the species can depend upon the isolation of the populations of hamsters in which melanism is present from other populations of the species. Thirdly, the ecological conditions in the regions where black hamsters are distributed may be favorable for them, whereas such conditions in other regions may be unfavorable, and consequently natural selection prevents the spread of the melanic form over the whole area of the species. Since these factors (diffusion, isolation, and natural selection) do not exclude each other, it may be that the distribution of black hamsters in the Ukraine is due to joint action of them all.

However, a number of considerations lead to the conclusion that diffusion and isolation have played at most a very insignificant part in limiting the distribution of black hamsters in the Ukrainian S.S.R. In the first place, the melanic mutation of the hamster is capable of spreading very rapidly under favorable conditions, because of the high reproductive rate of the hamster and because migrations frequently occur in this species (Novikov 1933, 1935). As will be shown later in this report, the boundary of the distribution of black hamsters in the Odessa region during the time of this study was undergoing a rapid displacement southward at a rate of about 30 km per annum. So, if a diffusion of the melanic mutation could occur freely, it should have spread over all the area of distribution of the species. However, this did not take place.

Moreover, it can be shown that in at least some parts of the area of distribution of the species in the Ukraine either no such expansion occurred of the region where melanics are found or its rate was in any case very slow. As has been already mentioned, black hamsters were found by KESSLER near Zolotonosha (Poltava region) in the middle of the 19th century. At present, after a lapse of nearly a hundred years, the boundary of the area of distribution of melanics lies at a distance of only 80 km from Zolotonosha. In other words, during the whole period since KESSLER's collections were made the territory occupied by black hamsters either remained in this part of the Ukraine without changes or at most underwent only an insignificant expansion. The absence of any gradient in the frequency of black hamsters in those regions of the Ukraine where they exist also speaks against a free diffusion of the melanic mutation from a definite center of origin.

It is also difficult to explain the absence of black hamsters in some parts of the area of the distribution of the species in the Ukraine by isolation of the populations inhabiting these parts from the populations of the regions where melanic hamsters are present. In the case of the hamsters, the role of isolating factors can be played by continuous and sufficiently wide spaces which are unsuitable for the life of this species or by such natural barriers as marshes, large surfaces of water, or mountain ranges. The data collected from hundreds of factories densely covering all the parts of the territory studied at this time show that hamsters are present throughout, with the possible exception of only the most northern part of the Zhitomir region, where lies the northern boundary of the distribution of the species. Thus, no large spaces exist in the Ukraine which are unsuitable for hamsters. Neither are natural barriers such as marshes, large surfaces of water, or mountain ranges present to separate the area where black hamsters are found from the surrounding territory. The only possible isolating factors which exist here are rivers. However, it is highly improbable that rivers may be responsible for the absence of black hamsters in some parts of the investigated territory. First of all, as may be seen in figure 1, the boundaries separating the districts where melanics are present from those where they are absent lie chiefly latitudinally, whereas the main rivers flow longitudinally. Furthermore, a detailed examination of these boundaries shows that they nowhere even roughly coincide with the large rivers. These boundaries cross a number of large rivers, as Dnieper, Desna, and Southern Bug. Literature data show that rivers in general cannot serve as effective obstacles for migration of hamsters. DUPON (1932), who studied the ways by which hamsters penetrated into Belgium, showed that in their westward movement they crossed the Rhine in historic times, and that at the end of the 19th and in the beginning of the present century they crossed a number of other rivers (for example, the Maas) and canals. NOVIKOV (1935) cites the statement of DUKELSKAIA that between 1930 and 1935 hamsters crossed the Yenisei which formed the eastern boundary of the species, and that during the several following years they populated the Minusinsk steppe lying some hundred kilometers to the east. It is known that hamsters swim well. Moreover, they fre-

quently wake from their winter sleep and run about, sometimes crossing frozen rivers during their peregrinations. Taking all this into consideration, we must agree with NOVIKOV (1935) who says that even such a large river as the Dnieper cannot serve as an isolating barrier for hamsters.

Thus, only the third explanation remains—namely, that ecological conditions in some parts of the investigated territory favor black hamsters, whereas in other parts these conditions are unfavorable. This assumption could be regarded as sufficiently well grounded only if it could be shown that such differences in the ecological conditions actually exist and that the boundary dividing the two ecological zones coincides more or less closely with that of the main area of distribution of black hamsters.

A careful comparison of the distribution of black hamsters in the Ukrainian S.S.R. with the maps of mean monthly and annual temperatures, of rainfall, and of soil, and geobotanical maps of the corresponding parts of the Ukrainian S.S.R., showed that the southern boundary of the distribution of black hamsters roughly coincides with the line separating the southern dry districts of the Ukraine (with an annual amount of precipitations less than 500 mm) from the northern more humid districts. Moreover, the area of distribution of black hamsters more or less coincides with the zone of degraded black soils; and lastly there is a close correlation between the distribution of black hamsters and the distribution of the forest-steppe vegetation. No clear connection was detected with other factors (temperature, snow-cover).

The most thorough geobotanical study of the Ukraine is that of LAVRENKO and POGREBNIAK (1930). On the basis of their descriptions of the botanical districts of the Ukraine and the map accompanying their paper, a fair picture of the limits of the zone of forest-steppe vegetation in the Ukrainian S.S.R. can be formed. As seen from the map in figure 1, the boundaries of the forest-steppe zone coincide fairly closely with the boundaries of the area of distribution of melanic hamsters in the Ukrainian S.S.R. This coincidence is more or less conspicuously disturbed only in three places: in the Zhitomir region the boundary of the area of distribution of black hamsters lies northward of the forest-steppe zone, and in the Odessa region and in the eastern part of the Kiev region it lies southward of the boundary of the forest-steppe zone. It should be noted, however, that the first two discrepancies are of very recent origin. In both cases the expanison of black hamsters beyond the forest-steppe zone occurred only during the last five or six years.

The opinion is frequently expressed that forms deviating from type are especially frequent near the borders of the distribution area of a species, where the latter meets with atypical environmental conditions (see, for example, REINIG 1938). However, in the case of melanic hamsters the situation seems to be reversed. The forest-steppe zone to which black hamsters are (at least in the Ukraine) confined is optimal for hamsters in general. This fits well with the observations of PETZSCH (1936) that the frequency of black hamsters is especially high in years when hamsters are numerous and falls when their number diminishes. In order to test these conclusions further, an attempt was made

to ascertain whether or not there is a connection between the existence of melanics and the population density of hamsters. Though the data of "Soiuspushnina" do not allow one to estimate the absolute number of hamsters inhabiting a given region or district, they give a rather precise picture of the relative density of the species. The great number of district factories, each

TABLE 5

Relative density of population of hamsters and frequency of melanics in some regions during 1935–1938.

REGION	PELTS PURCHASED PER ANNUM PER km^2	PERCENTAGE OF MELANICS
Kamenets-Podolsk	3.35	4.91
Poltava	1.07	7.80
Voroshilovgrad	0.04	0.04
Zaporozhie	0.10	0.01

purchasing pelts from dozens of trappers, tends to cancel the random fluctuations in the activities of individual trappers.

Among the 15 administrative regions of the Ukrainian S.S.R. observed in this study black hamsters are practically absent in two (Voroshilovgrad and Zaporozhie), and in two others are found nearly everywhere (Kamenets-Podolsk and Poltava). Table 5 shows the average number of hamster pelts purchased in these regions per square kilometer per year during the period 1935–1938 and the average percentage of melanics among them.

TABLE 6

Relative density of population of hamsters in districts where melanics were present and where they were absent in 1938.

REGION	DISTRICTS WHERE MELANICS WERE TRAPPED IN 1938		DISTRICTS WHERE NO MELANICS WERE TRAPPED IN 1938	
	NUMBER OF DISTRICTS	PELTS PURCHASED PER km^2 PER YEAR	NUMBER OF DISTRICTS	PELTS PURCHASED PER km^2 PER YEAR
Kamenets-Podolsk	28	4.10	5	1.45
Chernigov	15	6.34	16	5.09
Vinnitsa	6	2.01	26	1.40
Odessa	9	0.94	17	0.48

The density of population of hamsters is much higher in regions lying entirely within the area of distribution of melanics than in regions where black hamsters are rare or absent. The same regularity is seen within each region if we compare districts where melanics are present with those where they are absent. This is shown in table 6. Only districts where more than one hundred pelts were purchased in 1938 are included in this table.

The density of the population of hamsters is considerably higher in districts where melanics were found than in ones where they were absent in all four regions. A similar picture is observed in other regions of the investigated territory. Thus, the conclusion that the melanic form is favored especially in such localities where the conditions are optimal for the species in general seems to be warranted.

CAUSES OF THE DIFFERENT FREQUENCY OF BLACK HAMSTERS IN DIFFERENT LOCALITIES WITHIN THE MAIN AREA OF THEIR DISTRIBUTION IN THE UKRAINE

The variation in the frequency of black hamsters in individual districts due to sampling errors must be rather insignificant, since our material includes from one hundred to several thousands of pelts purchased annually in each of the district factories the records of which served for our analysis.

The analysis of the causes of the presence of melanic hamsters in some places and their absence in others showed the existence of ecological differences between these places. If the differences in the frequency of black hamsters within the area of their distribution are conditioned by causes similar in principle, we should expect to find ecological differences also between districts with high and with low frequencies of melanics. In order to detect such differences it was necessary to make a detailed comparison of the conditions prevailing in zones of high and of low frequencies of melanics. A study was undertaken of the Chernigov zone of high frequency of melanics. Especially thoroughly studied was the eastern boundary of this zone, in the vicinity of the town of Priluki and the villages Malo-Devitsa, Rudovka, Yablonovka, Perevolochnoie, Ivanitsa, and Srebonie, where the difference between the frequency of melanics inside and outside the boundary is particularly striking. This investigation showed that the boundary of the zone of high frequency of melanics established on the basis of the data of "Soiuspushnina" coincides very closely with a line of demarcation dividing this region into parts sharply differing in their ecological conditions. Westward of this line lies a marshy lowland with soils of the black type, whereas eastward the territory is hilly, much drier, and the soils contain a large admixture of clay. The contrast between these parts is very pronounced.

Thus, the investigation of the Chernigov zone of high frequency of melanics showed that the concentration of the melanic mutation is higher in marshy districts and lower in more dry districts with a hilly relief. Though no such studies were made in other zones of high frequency of melanics, microgeographic descriptions and detailed maps of the respective districts indicate that there exist similar situations. This is also confirmed by a number of experienced trappers with whom the question has been discussed.

We have seen above that black hamsters are usually present in districts with a high density of the hamster population and absent where this density is low. A similar difference in the densities of hamster populations exists between districts with high and with low frequencies of melanics. Table 7 shows the average numbers of hamster pelts per year per square kilometer purchased during the period 1935–1938 in different regions of the territory studied, and

the average frequencies of melanics in these regions during the same period. The data for 1934 and 1939 are excluded since they do not include all the investigated regions.

The data given in table 7 confirm the conclusion that the frequency of melanics is higher in places where hamsters are more abundant. Among the 15 regions studied, three regions characterized by the highest frequencies of me-

TABLE 7

Average number of hamster pelts per year per square kilometer purchased during 1935–1938, and average frequency of melanics during the same period in different regions.

REGION	PERCENTAGE OF MELANICS	NUMBER OF PELTS PER YEAR PER km²
1. Poltava	7.80	1.97
2. Kamenets-Podolsk	4.91	3.35
3. Chernigov	4.54	3.34
4. Kharkov	3.11	0.22
5. Zhitomir	2.98	0.58
6. Stalino	1.59	0.27
7. Kiev	1.42	0.87
8. Vinnitsa	0.85	1.29
9. Sumy	0.49	0.97
10. Nikolaev	0.33	0.12
11. Dniepropetrovsk	0.24	0.68
12. Odessa	0.09	0.26
13. Kirovograd	0.05	0.61
14. Voroshilovgrad	0.04	0.04
15. Zaporozhie	0.01	0.10

lanics (Poltava, Kamenets-Podolsk, and Chernigov) occupy the first, second, and fourth places according to the density of the hamster population, whereas the three regions characterized by the lowest frequencies of melanics (Kirovograd, Voroshilovgrad, and Zaporozhie) occupy the eighth, fourteenth and fifteenth places. The coefficient of correlation between the frequency of melanics and the relative density of hamster populations, calculated on the basis of the data of table 7, equals +0.54. However, this coefficient is statistically not quite significant ($P=0.05$) because of the small number of groups into which the material is divided. Another test was therefore made of the validity of this conclusion. The coefficient of correlation between the frequency of black hamsters and the relative density of the population of the species was calculated for all the 114 districts where melanics were found in 1938 and where the number of hamsters trapped during this year exceeded one hundred. This coefficient is somewhat lower than the analogous one for regions, equalling only 0.28, but is statistically reliable ($t=3.09$).

The chief enemy of hamsters in the Ukraine is the polecat (PIDOPLICHKA 1930b); a somewhat lesser role is played by the fox, and a still lesser one by the weasel, the latter killing only the young individuals. Among birds of prey only the largest species hunt hamsters, and these species occur but rarely in the

Ukraine. The data on the frequency of black hamsters in different regions of the Ukrainian S.S.R. were compared with the data of "Soiuspushnina" on the number of polecats (*Putorius putorius* L. and *Putorius eversmanni* Lesson.), foxes, and weasels trapped in the corresponding regions. Though these data cannot characterize the absolute frequency of these predators in different regions, they probably reflect their relative frequency, since they embrace very extensive material gathered in numerous localities with many trappers and hunters. Since the administrative regions of the Ukrainian S.S.R. vary in area, the frequencies of black hamsters were compared not with the absolute numbers of polecats, foxes and weasels trapped there, but with the ratios between the numbers of hamsters and the numbers of predators trapped. Such comparisons were made for the Voroshilovgrad, Dniepropetrovsk, Poltava, Stalino, Kharkov, and most of the Kirovograd region on the basis of the data for 1938, and for the remaining regions on the basis of the data for 1939. Calculations were made of the coefficients of correlation between the frequencies of melanics and the ratios number of hamsters/number of polecats, number of hamsters/number of foxes, and number of hamsters/number of weasels. It was found that a high positive correlation exists between the frequency of melanics and the ratio number of hamsters/number of polecats ($r = +0.51$) and a lower between the frequency of melanics and the ratio number of hamsters/number of foxes ($r = +0.30$). Either no correlation exists between the frequency of melanics and the ratio number of hamsters/number of weasels or it is insignificant. Thus, black hamsters are present chiefly in such places where the number of polecats and foxes is relatively small in comparison with the number of hamsters. However, this does not necessarily mean that these predators limit the frequency of black hamsters by differentially eliminating them because of their contrasting coloration or some peculiarities of their life habits. Such a conclusion would be justified only if it were shown that the connection between the frequency of melanics and the ratio of the number of hamsters and the number of predators is not a spurious one—that is to say, is not conditioned by an uneven distribution of hamsters on the background of a more or less even distribution of predators. In order to test this possibility, the partial coefficients of correlation between the frequency of melanics and the ratios number of hamsters/number of polecats and number of hamsters/number of foxes were calculated, excluding the influence of the density of the hamster population. These calculations showed that no real correlation exists between the frequency of black hamsters and the relative frequency of polecats and foxes. On the other hand, a calculation of the partial coefficients of correlation between the frequency of melanics and the density of hamster population excluding the influence of the frequency of polecats and foxes shows that a positive correlation is here quite obvious. Therefore, it is evident that the abundance of black hamsters in localities where the environment is optimal for their species is not conditioned by a more favorable relation between the number of hamsters and the number of their natural enemies. In order to reveal the actual causes of this connection, a more detailed study of the biological differences between black and usual hamsters is necessary.

A preliminary investigation was undertaken with the purpose of finding out whether there exist in the zones of high frequency of melanics places especially favored by black hamsters or whether the animals are distributed in these zones more or less evenly. Table 8 presents the records of 26 trappers in the neighborhood of several villages in the Yablonovka district (Chernigov region) on May 3, 1941. These results were checked by the author, who was at the time present at the district factory of "Soiuspushnina."

The analysis of the data presented in table 8 does not allow a definite conclusion about the existence of real differences in the frequency of black hamsters in the vicinity of the villages studied, since these differences are statistically not quite significant, but it suggests their probability.

Further, a territory of about four km² near the village Yablonovka was selected and examination was made of the hamsters caught there during the

TABLE 8

Results of trapping hamsters in the vicinity of several villages in the Yablonovka district.

VILLAGE	TOTAL HAMSTERS TRAPPED	BLACK HAMSTERS TRAPPED	PERCENTAGE OF BLACK
Yablonovka	101	14	13.9
Dubovyi Gai	112	31	27.7
Bubnovshchina	59	14	23.7
Sergeievka	87	13	14.9
Rudovka	102	26	25.5
Total	461	98	21.3

11th and 12th of May, 1941, in traps placed in various micro-ecological stations. In all, 26 hamsters were caught (all adults), which were distributed as follows: on a maize field—eight normal and three black; on a mulberry plantation—three normal and one black; on an old thrashing-floor near a tobacco plantation—two normal; on a field prepared for the sowing of potatoes—five normal and four black.

It may be concluded that in the zones of high frequency of melanics black hamsters are intermingled with usual ones, though their frequency in different localities within these zones may vary rather considerably. Lastly, we must consider the four small "islands" of black hamsters which lie outside the main area of distribution of melanics in the Ukrainian S.S.R. Data about hamsters trapped there during the investigated period are given in table 9.

In the Zaporozhie and Chernigov "islands" only single black hamsters were trapped during the period studied. In the Stalino and Nikolaev "islands" black hamsters were met in considerable numbers and on the territory of two adjacent districts. The Zaporozhie "island" is separated from the main area of distribution of black hamsters by a large territory including numerous factories of "Soiuspushnina" where no melanics were recorded among many thousands of hamsters trapped during the investigated period. The possibility of the

immigration of a black individual from the main area can therefore be excluded. The Chernigov "island" lies much nearer to the main area of distribution of melanics, and the possibility of immigration of a black individual from this area is to be reckoned with. However, the absence of black hamsters in several intermediate points speaks against this possibility and makes it probable that the black individual found in this "island" also arose independently of the main area of distribution of melanics. The Nikolaev and Stalino "islands," like the Zaporozhie one, are separated from the main area of distribution of black hamsters by large territories where no melanics were found. It is

TABLE 9

Hamsters trapped in the "islands" of melanics in the Ukrainian S.S.R.

REGION WHERE THE "ISLAND" IS LOCATED	NUMBER OF DISTRICTS IN THE "ISLAND"	1934		1935		1936		1937		1938		1939		TOTAL	
		TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK	TOTAL	BLACK
Chernigov	1	No data		11,328	1	7,971	0	No data		11,385	0	8,274	0	38,958	1
Zaporozhie	1	447	1	181	0	356	0	127	0	126	0	No data		1,237	1
Stalino	2	11,618	765	2,198	17	4,390	29	3,202	0	698	0	No data		21,106	811
Nikolaev	2	No data		208	0	611	0	1,472	47	553	0	574	0	3,465	47

therefore also highly probable that melanism arose in these two "islands" independently of the main area. The black mutants which appeared here found conditions which allowed them to reproduce, giving a significant frequency of melanics in the corresponding populations.

CAUSES OF DIFFERENT FREQUENCIES OF BLACK HAMSTERS IN DIFFERENT DISTRICTS OF THE BASHKIRIAN A.S.S.R.

The analysis of the distribution of black hamsters in the Ukraine showed that the differences in the frequency of melanics in different localities are connected with the ecological peculiarities of the latter and are probably caused by natural selection. It seems that a similar situation exists in Bashkiria. The differences in the frequency of melanics in different parts of Bashkiria can be explained neither by accidental fluctuations in the survival and reproduction of the two investigated forms of hamsters, nor by isolation. Against the first assumption speaks the continuity of both the whole distribution area of melanics and of the zone of their high frequency. With regard to isolation, it is necessary to point out that though Bashkiria is rich in mountain ranges, some of which might possibly act as barriers for hamsters, these mountain ranges nowhere coincide with the boundaries of melanics. An analysis of detailed maps of Bashkiria shows that no other natural barriers coincide with these boundaries. The only possible exception is the western boundary of the zone of high frequency of melanics which partly (between Birsk and Ufa) coincides with the course of the river Belaia. However, since both southward and north-

ward from this region the percentages of melanics on both sides of the Belaia are very nearly equal, it is hardly probable that the differences in the frequency of black hamsters in Bashkiria are even partially conditioned by isolation.

Two possible explanations remain. Either the black mutation is more or less freely "diffusing" from some center or the differences in the frequency of black hamsters in different districts are created by natural selection. The first of these explanations is highly improbable, since black hamsters have been known in Bashkiria for over 160 years and the black mutation is capable of spreading very rapidly (GERSHENSON in press).

A detailed comparison was undertaken of the map of distribution of black hamsters in Bashkiria with topographic maps, maps of mean monthly and annual temperatures and precipitations, soil and geobotanical maps.[2] This comparison showed that black hamsters are found in Bashkiria chiefly in regions with an annual precipitation of 500 mm or higher and on degraded black soils, the situation resembling that seen in the Ukraine. Further, it was found that all the districts with a high frequency of melanics are located in the lowlands of Bashkiria (elevation less than 200 meters); in the elevated northeastern part (Ufa plateau) and southwestern part (Common Syrt) black hamsters are rare. In the southeastern part lying in the region of the Ural mountain range (elevation more than 600 meters) black hamsters are absent or rare. Finally, a connection was found between the frequency of black hamsters and the type of vegetation. The territory of the Bashkirian A.S.S.R. can be divided into the following six regions, the boundaries of which are shown in figures 4 and 5 (1) The humid forest-steppe region is characterized by a level relief, annual atmospheric precipitations of 500–550 mm, and degraded black soils. It abounds in broad-foliage woods and groves. (2) T he dry forest-steppe region intermediate between the humid forest-steppe and the steppe regions; it has a hilly relief, a smaller annual precipitation (350–400 mm), and rich black soil. Woods are scarce. (3) The mountain forest-steppe region is intermediate between the humid forest-steppe and forest regions and is located chiefly on the slopes of the smaller Pre-Ural mountain ranges. (4) The steppe Pre-Ural region is a typical level black-soil steppe region with 300–350 mm of atmospheric precipitations annually. (5) The steppe Trans-Ural region is an arid steppe region, largely with a hilly and even mountainous relief. (6) The mountain forest region is located on the Ural mountain range and on the neighboring minor mountain ranges. The extreme southwestern part of this region (between the rivers Belaia and Sakmara) is less densely covered with forests and resembles the mountain forest-steppe region.

As may be seen from figures 1 and 2, the zone of high frequency of black hamsters coincides with the humid forest-steppe region. A much lower fre-

[2] The following chief sources were used: "The Great Soviet World Atlas," Vol. I (1937), "The Ural Soviet Encyclopedia," Vol. I (1933), the official edition "The Bashkirian A.S.S.R." (1939), the works of NOVOPOKROVSKY (1931), and of IVANOV (1937) and the unpublished detailed soil and geobotanical maps of Bashkiria prepared by the BASHKIRIAN AGRICULTURAL RESEARCH STATION.

quency of black hamsters characterizes the dry forest-steppe region, and in all the other geobotanical regions of Bashkiria melanics are either rare or absent. These conclusions were further verified by three trips undertaken by the writer into the western, southern and northeastern parts of the country during which field observations on hamsters were carried out and a number of local trappers were interviewed. In Bashkiria, as in the Ukraine, black hamsters are adapted to definite ecological conditions—namely, to the forest-steppe regions and particularly to their most humid and low lying parts.

In the Ukraine the black hamsters are most frequent in localities with a high population density, where the environment is expecially favorable. To ascertain whether a similar situation exists in Bahskiria, we calculated the coefficient of correlation between the mean percentages of black hamsters in all the districts of Bashkiria and the mean numbers of hamster-pelts purchased annually per square kilometer by the local factories of the corresponding districts and found $r = +0.70 \pm 0.80$. Thus, the conclusion about the high frequency of black hamsters in places with a high density of hamster population holds for Bashkiria also. Hamsters in Bashkiria are in general more abundant than in the Ukraine, and the overall frequency of black is greater in Bashkiria.

SUMMARY

The dominant melanic form of hamster (*Cricetus cricetus* L.) presents favorable material for studies on the mechanisms of natural selection. An analysis of the distribution of black hamsters trapped in the Ukrainian S. S. R. and in Bashkiria is reported. It is based on data concerning approximately two million hamsters trapped in the Ukraine chiefly in 1934–1939, and more than one million trapped in Bashkiria during May–August, 1933, and the years 1937–1939.

In the Ukraine, as well as in Bashkiria, black hamsters are present in only a part of the total area, and the area where the melanics occur is practically continuous. Inside the area where melanics occur there are discrete nuclei in which their frequencies are especially high. The presence of black hamsters in some and their absence in other localities cannot be explained either by chance survival, by diffusion from a center of origin, or by isolation. The geographic differentiation of the population of the hamster with respect to the frequency of the black form is most probably caused by a differential fitness of melanics in diverse ecological conditions in the different districts. This differentiation is brought about by natural selection. This view is confirmed by the fact that the boundaries of the area of distribution of black hamsters in the Ukraine coincide fairly closely with the limits of the forest-steppe vegetation. In Bashkiria, black hamsters are most frequent in the more humid forest-steppe region and are rare or absent in the steppe, forest, and mountain regions.

The frequency of the melanics is correlated positively with the density of the total hamster population. No connection was found between the frequency of black hamsters and the abundance of their principal mammalian enemies.

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EVOLUTIONARY STUDIES ON THE DISTRIBUTION AND DYNAMICS OF MELANISM IN THE HAMSTER (CRICETUS CRICETUS L.). II. SEASONAL AND ANNUAL CHANGES IN THE FREQUENCY OF BLACK HAMSTERS

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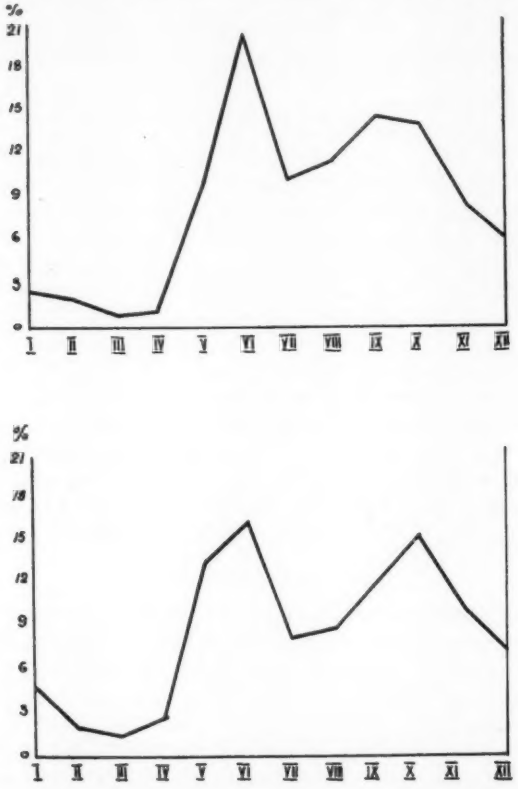
THE RECENT work of TIMOFEEFF-RESSOVSKY (1940) on dimorphic populations of Adalia, as well as the work of DOBZHANSKY (1943) and some unpublished data of our laboratories on wild populations of Drosophila, has shown that the composition of wild populations may undergo variations from season to season, these variations being conditioned by seasonal changes in the adaptive value of the genetic variants present in the population. Seasonal fluctuations in the dimorphic populations of the hamster (*Cricetus cricetus* L.) are reported in the present article. Although extensive data (GERSHENSON 1945) on the frequencies of black hamsters in various regions of the Ukraine and Bashkiria show these frequencies to be more or less constant, from year to year, nevertheless a detailed analysis of the data reveals significant alterations, more pronounced in some than in other parts of the distribution area. Since the frequency of black hamsters is controlled primarily by natural selection, a study of these seasonal and annual changes may be used to obtain an idea about the activity of natural selection in the species under consideration.

MATERIALS AND METHODS

We had at our disposal the data of fur factories of "Soiuspushnina" concerning the numbers of hamster pelts purchased monthly in some regions of the Ukrainian S. S. R. in 1936–1939, and in all of Bashkiria during 1937–1939 (GERSHENSON 1945). Only a part of this mass of data however, was suitable for examination of the seasonal changes in the frequencies of the black hamsters—namely data in which the total numbers of hamsters trapped each month and the numbers of blacks among them are sufficiently high to avoid statistical errors that might lead to erroneous conclusions. These requirements are met by the data for the Poltava, Chernigov, and Kamenets-Podolsk regions of the Ukraine and for Bashkiria. The data for Poltava region covered the period from the beginning of 1935 to the end of 1938, for Chernigov from the middle of 1935 to the end of 1939, and for Kamenets-Podolsk and for Bashkiria from the beginning of 1937 to the end of 1939.

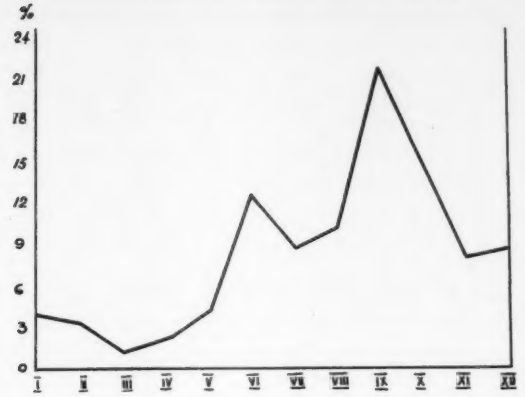
It is evidently necessary to know how much time elapses on the average between trapping the hamsters and selling their pelts to the factories of "Soiuspushnina." Two ways were used to solve this problem, namely a questionnaire was distributed among a large number of the trappers and fur agents in the territories concerned, and a study was made of the seasonal changes in the

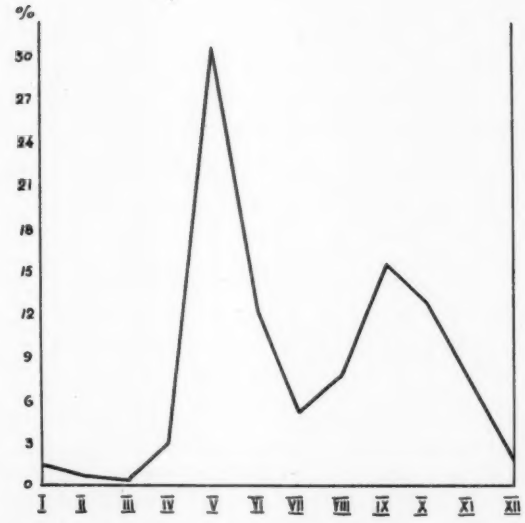
numbers of pelts purchased by the local factories of "Soiuspushnina." The answers to the questionnaire showed that hamsters are trapped in the Ukraine and in Bashkiria from the second half of April to the end of October, particularly at the beginning and at the end of this period. In midsummer, from about June 15 to August 15 in the Ukraine and from July 1 to September 1 in



FIGURES 1 and 2. Seasonal variations in the numbers of hamster pelts purchased by the district factories in various regions. The curves show mean numbers of pelts purchased during each month in percentage of the total number of pelts purchased during the whole year. Figure 1 (above).—Poltava region in 1935–1938 (total number of pelts 147,461). Figure 2 (below).—Chernigov region in 1935–1939 (total 579,355).

Bashkiria, relatively few hamsters are trapped because their favorite habitats, the cultivated fields, are inaccessible, and because most of the trappers are occupied by agricultural work. Furthermore, hamster pelts in summer are of inferior quality and are sold at lower prices. The pelts are sold usually within a month from trapping, except those trapped in autumn. However, even the





FIGURES 3 (above) and 4 (below). Seasonal variations in the numbers of hamster pelts purchased by the district factories in the Kamenets-Podolsk region in 1937–1939 (total pelts 216,157) and in Bashkiria in 1937–1939 (total 1,055,495), respectively.

autumn pelts are almost always sold before the beginning of the spring trapping season, so that little overlapping of the seasons takes place in the receipt of the pelts by the factories.

The data on the numbers of hamster pelts bought by the district factories of "Soiuspushnina" in different months of the year are summarized in figures 1–4. The seasonal variations are in all important respects similar in all the

regions of the Ukraine from which data are available as well as in Bashkiria. Relatively few pelts are sold to the factories from January to March; these are the pelts obtained in autumn, the selling of which was delayed. In April the number of pelts remains low, though it is somewhat higher than in March; this is probably explained by admixture of fresh pelts obtained from spring trapping which begins in this month. In May and June the numbers of pelts rise very sharply owing to the full development of trapping. A decrease in July and August is caused by less extensive trapping during the summer months. Finally, the number of pelts increases again in September and October, and

TABLE 1

Seasonal fluctuations in the frequency of black hamsters in Poltava region in 1935–1938.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	I–IV	1,339	394	29.42±1.26
	V–VI	7,397	1,187	16.05±0.42
1935	VII–VIII	4,264	438	10.27±0.47
	IX–X	4,531	504	11.12±0.49
	XI–IV	4,501	658	14.62±0.53
	V–VI	7,639	612	8.01±0.31
1936	VII–VIII	7,418	492	6.63±0.29
	XI–X	7,817	665	8.51±0.32
	XI–IV	7,875	884	11.23±0.35
	V–VI	16,748	1,343	8.02±0.21
1937	VII–VIII	9,411	327	3.47±0.19
	IX–X	14,198	774	5.45±0.19
	XI–IV	9,986	843	8.44±0.28
	V–VI	12,300	614	4.99±0.20
1938	VII–VIII	9,646	283	2.93±0.17
	XI–X	15,518	750	4.83±0.17
	XI–XII	5,973	421	7.05±0.33

drops sharply at the end of the trapping season in November and December.

The results of the questionnaire and the study of the seasonal dynamics of the numbers of hamster pelts purchased by the fur factories agree quite well. On the basis of these results, we divided the records of the district factories into the following four groups: (1) May–June, (2) July–August, (3) September–October, (4) November–April of the next year. The data for the first period reflect fairly accurately the results of the spring trapping; the few autumn pelts which in rare cases are included into the data for May may safely be disregarded, since they are very few compared to the pelts obtained in spring. The data for the second and the third periods are less exact since they reflect not only the results of the corresponding months but also include admixtures of pelts obtained earlier in the year. The data for the fourth period reflect nearly exclusively the results of the last months of the trapping season.

SEASONAL FLUCTUATIONS IN THE FREQUENCY OF BLACK HAMSTERS IN THE UKRAINIAN S.S.R.

Table 1 and figure 5 contain the data on the seasonal fluctuations of the frequency of black hamsters in the Poltava region of the Ukrainian S.S.R. in 1935–1938.

The percentage of melanics among hamsters trapped in this region is subject to very considerable seasonal fluctuations, the nature of which remains constant from year to year. Every year the percentage of black hamsters falls in winter, so that their frequency in spring is lower than in the previous autumn. A less marked decrease of the frequency of melanics continues during spring and the first half of summer, and reaches its minimum in July–August, after which a moderate increase takes place during the autumn months. These seasonal differences are statistically significant.

The data show that under the conditions existing in the Poltava region the relative fitness of melanics is different at different seasons of the year. Obviously, in winter the mortality of melanics is higher than the mortality of usual hamsters. The decrease in the frequency of melanics during winter can be explained only by differential elimination, no reproduction taking place during this season. If the viability of usual hamsters during the winter period be taken as unity, then the viability of melanics will be 0.44 for the winter of 1934–35, 0.51 for the winter of 1935–36, 0.69 for the winter of 1936–37, and 0.56 for the winter of 1937–38.

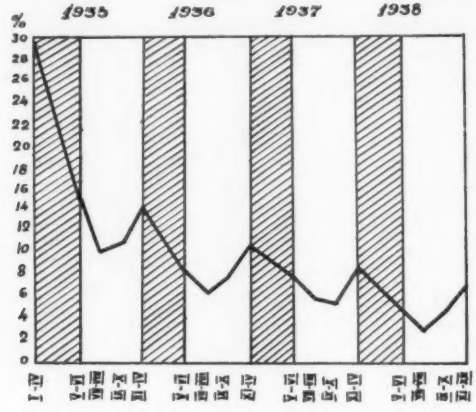
The decrease in the frequency of the melanics in July and August may be either real or only apparent. In spring and in autumn hamsters are trapped wherever they can be found, while in summer practically no trapping is done on cultivated fields. Though no data are available showing that the percentage of melanics is higher on cultivated fields than elsewhere, this possibility is not excluded. The decrease in the proportion of black pelts among hamster pelts bought by the district factories in July and August might be caused by the trapping of hamsters chiefly in such habitats where melanics are comparatively less frequent.

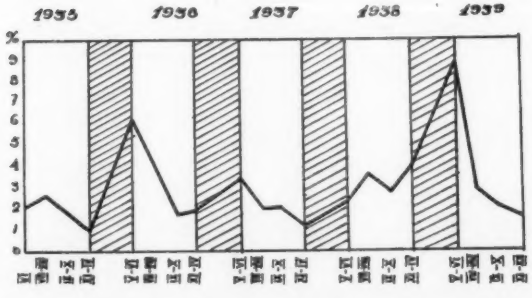
Quite different from the seasonal variations in the Poltava region are those in the Chernigov region (table 2 and fig. 6). Here the frequencies increase every winter. This can be explained only by a lower winter mortality of black as compared with that of usual hamsters. If the viability of usual hamsters during the winter period be taken as unity, then the viability of melanics will be 7.05 for the winter of 1935–36, 2.05 for the winter of 1936–37, 1.95 for the winter of 1937–38, and 2.50 for the winter of 1938–39. The fluctuations of the frequency of black hamsters in summer are less regular. In four out of the five years studied, a decrease in the frequency of melanics occurred in summer and autumn months, but in the summer of 1938 it was somewhat increased.

Data about the seasonal fluctuations of the frequency of black hamsters in the Kamenets-Podolsk region are given in table 3 and in figure 7.

In winter a rather considerable increase in the frequency of melanics takes place, caused by their lower relative winter mortality. If the viability of usual

hamsters during the winter period be taken as unity, then the viability of melanics will be 2.11 for the winter of 1936–37, 1.11 for the winter of 1937–38, and 1.16 for the winter of 1938–39. In summer the frequency of melanics in the Kamenets-Podolsk region somewhat decreases, as it does in the Chernigov region. A feature not seen in Chernigov is a rather pronounced drop in the

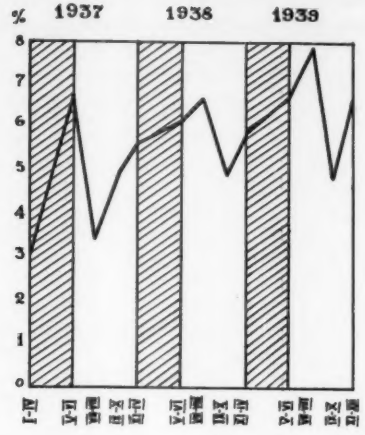


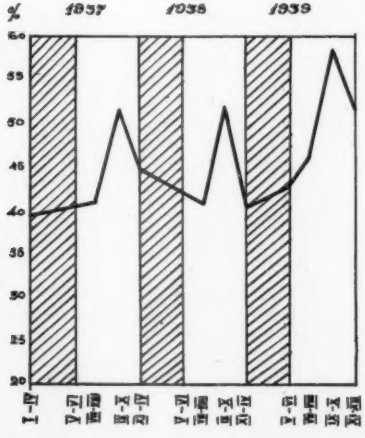


FIGURES 5 (above) and 6 (below). Seasonal fluctuations in the frequencies of black hamsters. Shaded columns indicate the winter periods. Figure 5.—Poltava region. Figure 6.—Chernigov region.

frequency of black hamsters in Kamenets-Podolsk in September–October, counterbalanced by an increase in their frequency in the following months.

Summarizing the data on the seasonal fluctuations of the frequency of black hamsters in the Ukrainian S.S.R., it is seen that in all regions from which such data were available these fluctuations are considerable and fairly regular. Most characteristic are the changes which take place in winter. In the Chernigov and Kamenets-Podolsk regions, where a continuous general increase in





FIGURES 7 (above) and 8 (below). Seasonal fluctuations in the frequencies of black hamsters. Shaded columns indicate the winter periods. Figure 7.—Kamenets-Podolsk region. Figure 8.—Bashkiria.

the frequency of melanics took place during the period studied (see below), this increase was caused by a lower relative winter mortality of melanics. In the Poltava region, where, during the period studied, the general frequency of melanics continuously decreased, this was caused by a higher relative winter mortality of the melanics. The summer changes of the frequency of melanics

TABLE 2

Seasonal fluctuations of the frequency of black hamsters in the Chernigov region in 1935–1939.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	VI	20,257	396	1.95±0.10
1935	VII–VIII	17,098	396	2.32±0.11
	IX–X	23,216	386	1.66±0.09
	XI–IV	14,859	143	0.96±0.08
	V–VI	20,185	1,293	6.41±0.28
1936	VII–VIII	13,801	543	3.93±0.17
	IX–X	24,417	392	1.61±0.09
	XI–IV	19,412	351	1.81±0.10
	V–VI	15,526	550	3.54±0.18
1937	VII–VIII	12,379	268	2.16±0.13
	IX–X	38,772	797	2.06±0.07
	XI–IV	31,538	369	1.17±0.06
	V–VI	33,192	747	2.25±0.08
1938	VII–VIII	25,096	931	3.71±0.12
	IX–X	62,351	1,758	2.82±0.07
	XI–IV	6,808	2,532	3.69±0.08
	V–VI	69,894	6,110	8.74±0.11
1939	VII–VIII	38,078	1,178	3.09±0.09
	IX–X	23,061	535	2.32±0.09
	XI–XII	7,615	138	1.81±0.16

TABLE 3

Seasonal fluctuations of the frequency of black hamsters in the Kamenets-Podolsk region in 1937–1939.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	I–IV	14,769	452	3.06±0.014
	V–VI	15,470	1,030	6.66±0.20
1937	VII–VIII	18,434	625	3.39±0.14
	IX–X	30,966	1,517	4.90±0.12
	XI–IV	17,330	969	5.59±0.016
	V–VI	6,958	428	6.15±0.28
1938	VII–VIII	7,511	495	6.59±0.29
	IX–X	30,633	1,512	4.94±0.12
	IX–IV	25,700	1,528	5.95±0.15
	V–VI	14,314	960	6.71±0.21
1939	VII–VIII	12,230	954	7.80±0.25
	IX–X	13,678	667	4.88±0.19
	XI–XII	8,164	558	6.83±0.28

were on the whole less regular than the winter ones; as a rule these changes occur in a direction opposite to that of the changes taking place in winter.

SEASONAL FLUCTUATIONS IN THE FREQUENCY OF BLACK HAMSTERS IN THE BASHKIRIAN A.S.S.R.

Data about seasonal fluctuations of the frequency of black hamsters in Bashkiria are presented in table 4 and in figure 8. The fluctuations here differ considerably from those observed in the Ukraine. In the winters of 1936–37 and 1938–39 the percentage of black hamsters somewhat increased, whereas in the winter of 1937–38 it decreased slightly. The relative viability of melanics is 1.11

TABLE 4

Seasonal fluctuations of the frequency of black hamsters in the Bashkirian A.S.S.R.

YEARS	MONTHS	TOTAL HAMSTERS	BLACK HAMSTERS	PERCENTAGE OF BLACK
	I–IV	7,701	2,981	38.71±0.60
1937	V–VI	78,041	31,080	41.11±0.17
	VII–VIII	10,216	4,515	42.24±0.49
	IX–X	105,238	56,357	53.53±0.15
	XI–IV	79,372	35,863	45.18±0.18
	V–VI	182,652	80,398	44.02±1.12
1938	VII–VIII	109,548	45,885	41.89±0.15
	IX–X	183,554	97,922	53.35±0.12
	XI–IV	64,261	26,483	41.21±0.19
	V–VI	195,887	89,582	45.73±0.11
1939	VII–VIII	15,314	7,249	47.34±0.40
	IX–X	19,545	11,199	57.30±0.37
	XI–IV	4,040	2,140	53.19±0.78

for the winter of 1936–37, 0.98 for the winter of 1937–38, and 1.20 for the winter of 1938–39. During most of the spring and summer months the frequency of melanics varies more or less irregularly, but an increase takes place at the end of every summer, which is followed by a drop in autumn.

An analysis of the seasonal fluctuations in Bashkiria shows clearly how cautious one must be in determining the intensity and direction of natural selection on the basis of mean annual data. In the Poltava, Chernigov, and Kamenets-Podolsk regions of the Ukraine the relative numbers of hamster pelts purchased by the fur factories during each of the periods into which the year has been divided remain more or less constant from year to year. Not so in Bashkiria. The relative numbers of hamster pelts purchased in May–June of 1939 was very high (84 per cent of all the pelts purchased during this year) as compared with the numbers of pelts purchased in the corresponding periods of 1937 (29 per cent) and of 1939 (34 per cent). Since the percentage of melanics in May–June is comparatively low in Bashkiria, this leads to a decrease in the

mean annual frequency of black hamsters for 1939 (46.14 per cent of melanics as compared with 46.41 per cent in 1938 and 47.54 per cent in 1937). However, the curve shown in figure 8, as well as a comparison of the data for 1937–1939 with the data on the frequency of melanics in Bashkiria in 1933 (GERSHENSON, in press), leads to the conclusion that this decrease in the frequency of melanics in Bashkiria is only apparent and that in reality a rather rapid increase in their frequency was taking place during this period.

GENERAL TRENDS IN THE FREQUENCIES OF BLACK HAMSTERS IN THE UKRAINE

The data on the frequencies of black hamsters in different regions and districts of the Ukrainian S.S.R. (GERSHENSON 1945) show that these frequencies do not remain absolutely constant from year to year but show some significant changes. Furthermore, it is noteworthy that in some parts of the Ukraine a general increase and in other parts a decrease was observed. The first of these tendencies predominates, so that the frequency of black hamsters in the Ukraine taken as a whole has markedly increased during the period of observation.

If the districts in which the frequencies of black hamsters have significantly increased, decreased, or remained stationary are plotted on a map of the Ukraine, it becomes clear that these three classes of districts are not distributed at random but form practically continuous zones. One zone is characterized by a general increase, another by a decrease, whereas the relatively few districts which showed a constant frequency of black hamsters are located mostly between the first two zones. The zone in which the percentage of black hamsters increased during the period of investigation includes the Vinnitsa, Zhitomir, Kamenets-Podolsk, Kiev, and Odessa regions, parts of the Dniepropetrovsk and Kharkov regions, and small parts of the Sumy and Poltava regions, thus occupying chiefly the western part of the territory studied. The other zone, characterized by the decrease in the frequency of melanics, lies entirely in the eastern part of this territory and includes the Stalino region, nearly all the Sumy and Poltava regions, and parts of the Kharkov and Dniepropetrovsk regions. Moreover, it probably includes the Voroshilovgrad region, where the frequency of melanics is too low to allow any safe conclusions.

The fact that both an increase and a decrease in the frequency of melanics characterized continuous zones leads to the supposition that each of these two tendencies is conditioned by some general factors operating over large territories. However, an examination of the annual changes in individual regions shows that these tendencies may be realized in a highly diverse fashion even in regions located closely to one another, so that, for example, in two neighboring regions, both of which are characterized by a general increase in the frequency of melanics during the period studied, the intensity and even the direction of natural selection of melanics during individual years may vary practically independently. It is thus evident that besides general factors operating on large territories and controlling the main course of natural selection, important factors of a more local type exist which determine the mode of realization

of these general tendencies in each given place and at each given time. These local factors will be discussed in a later part of the present paper.

Highly noteworthy is the fact that in all the regions where a general increase in the frequency of black hamsters occurred during the investigated period, a steady extension of the area of distribution of melanics took place. This is clearly seen in figures 9 and 10, where the boundaries of the area of distribution of melanics in the Odessa and Chernigov regions respectively are shown for each of the five years studied. Especially rapid was the extension of the area of distribution of melanics in the Odessa region, where the southern boundary of this area was shifted approximately 150 kilometers southward during the period 1935–1939. A similar situation was observed also in the Vinnitsa, Kamenets-Podolsk, Kiev and Zhitomir regions. The extension of the area of distribution of melanics took place in all these regions in a "tongue-shaped" fashion—that is, the area was extended only in one or a few directions without losing its continuity. This last fact is important since it shows once more (see GERSHENSON 1945) that chance survival plays no important part in the geographical distribution of black hamsters.

In the regions where a significant general decrease in the frequency of black hamsters occurred during the investigated period, a reverse process took place —that is a reduction of the area of distribution of melanics. This may be seen especially well in the Stalino region, where melanics completely disappeared toward the end of the period of investigation; a similar change was observed also in the Sumy region, in a part of the Kharkov region, and probably in a part of the Dniepropetrovsk region. The insufficient number of factories in these regions from which statistically-significant data were available prevents as detailed an analysis of this process as it was possible to make in the cases of the extension of the area of distribution of melanics.

THE INTENSITY OF NATURAL SELECTION OF MELANICS IN DIFFERENT PARTS OF THE UKRAINE

To understand the role of natural selection in the transformation of wild populations, it is necessary to know the intensity with which it operates. Few data on the question exist in the literature, and most of the investigators who discuss the mechanisms of natural selection assume arbitrary values characterizing the intensity of natural selection, usually assuming that this intensity is very low.

We determined the intensity of natural selection of black hamsters by means of the formula proposed by HALDANE (1932)

$$k = P_{n+1} - P_n / P_{n+1} q_n^2$$

where k is the coefficient of natural selection, P_n is the concentration of the dominant allele in the n-th generation, q_n the concentration of the recessive allele in the same generation, and P_{n+1} the concentration of the dominant allele in the next generation. If the value of k is positive, it means that selection favors the dominant allele (in this case melanism); if it is negative it means

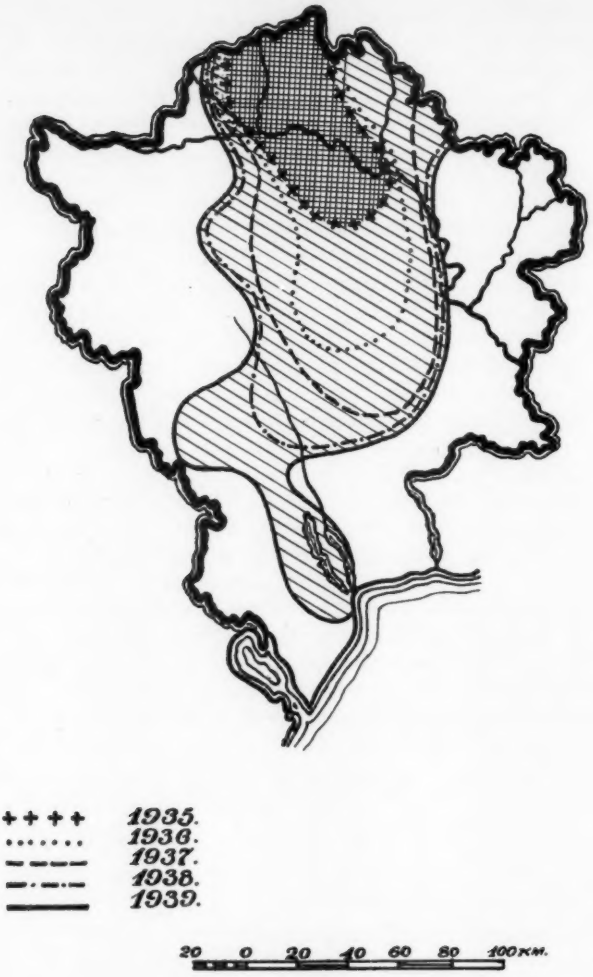


FIGURE 9. Extension of the area of distribution of black hamsters in the Odessa region in 1935–1939. Based on data from 42 factories each year.

that selection proceeds in the opposite direction. The value of k may vary between $k = +1$ and $-\infty$.

The above formula is deduced for cases when no overlapping of generations occurs. When generations overlap, as is the case in hamsters, a correction may be introduced. However, this correction holds only when the coefficient of selection is small, which is not the case in the present material, as will be

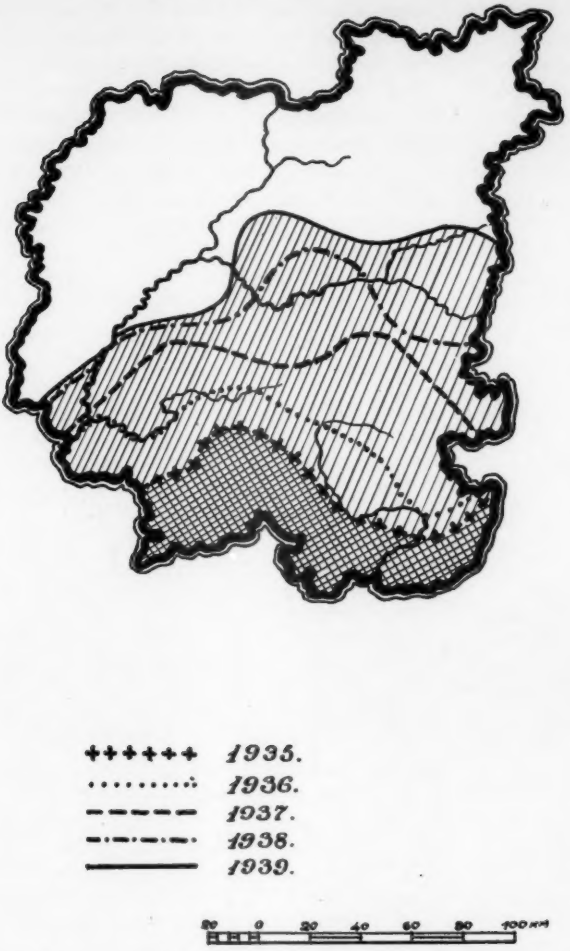


FIGURE 10. Extension of the area of distribution of black hamsters in the Chernigov region in 1935–1939. Based on data from 43 factories each year.

presently shown. Consequently, an exact determination of the values of k for the data here is impossible. All that can be done is to determine the approximate values of the coefficient of natural selection of melanics.

As was shown by PIDOPLICHKA (1928 and personal communication), hamsters reach in nature a maximum age of four to six years; this was found on the basis of a comparison of the condition of the teeth of the oldest hamsters trapped in nature with the condition of the teeth of hamsters kept in captivity

whose exact age was known. There can be no doubt that very many wild hamsters perish before reaching this age limit. In calculating the coefficients of selection we may proceed from the supposition that hamsters reproduce in nature only during one year and then perish; in this case the coefficients of selection obtained will be lower than the actual ones. On the other hand, we may proceed from the supposition that hamsters reproduce in nature during the entire potential period of their life—that is, approximately during five years; in this case the coefficients of selection obtained will be higher than the actual ones. The actual coefficients of selection will lie between these minimal

TABLE 5

Minimal and maximal coefficients of natural selection of black hamsters in different regions of the Ukraine.

REGION	TOTAL NUMBER OF HAMSTERS	NUMBER OF BLACK HAMSTERS	MINIMAL COEFFICIENTS OF SELECTION					MAXIMAL COEFF. OF SELECTION
			1934–35	1935–36	1936–37	1937–38	1938–39	
Vinnitsa	155,586	1,683	No data	0.98	−0.86	0.94	0.44	0.99
Dniepropetrovsk	118,448	248	0.72	−0.32	0.81	−0.02	No data	0.75
Zhitomir	82,996	2,580	No data	0.89	−0.29	−0.34	0.39	0.89
Kamenets-Podolsk	333,002	16,140	No data	0.66	0.18	0.14	0.11	0.82
Kiev	188,127	3,180	No data	0.57	0.14	0.12	0.25	0.76
Odessa	39,700	471	No data	0.58	0.20	0.67	−0.06	0.88
Poltava	167,848	13,756	0.18	−0.56	−0.40	−0.34	No data	1.39
Stalino	41,821	1,211	−0.63	−0.52	0.79	Negative	No data	Negative
Sumy	97,371	498	−0.82	0.83	0.20	−0.24	No data	−0.31
Kharkov	32,956	903	0.72	0.30	0.11	−0.33	No data	0.76
Chernigov	582,533	19,813	No data	0.57	−0.56	0.29	0.23	0.58

and maximal values, probably somewhat nearer to the minimal ones. For the sake of brevity, the coefficients of selection calculated by the first method (comparison of adjacent years) will be designated "minimal coefficients of selection" and those calculated by the second method (for the five-year period) "maximal coefficients of selection."

In table 5 are given the minimal coefficients of selection of melanics for all the investigated regions of the Ukraine except the Zaporozhie, Voroshilovgrad, Kirovograd, and Nikolaev regions, where the frequency of melanics was too low to allow such calculations.

It is necessary to note that the coefficients of selection presented in table 5 are somewhat more nearly exact for the Kamenets-Podolsk, Kiev, Poltava, and Chernigov regions than for all others. As shown previously (GERSHENSON 1945), determination of the coefficients of selection on the basis of mean annual data is not quite exact, since the frequency of melanics is subject to marked seasonal fluctuations. The relative number of hamsters trapped in each season

may vary from year to year. Therefore, for regions from which data was available on the frequency of black hamsters at different seasons—namely, for Kamenets-Podolsk (1937–1939), Kiev (1935–1939), Poltava (1935–1938) and Chernigov (1935–1939)—the mean of the frequencies of melanics at different seasons (see GERSHENSON 1945) was taken as the mean annual frequency of melanics used for the determination of the coefficients of selection. However, it should be noted that the relative number of hamsters trapped at different seasons in the Ukraine varies relatively little from year to year, so that the correction introduced by the described method is comparatively small. This may be illustrated by a comparison of the maximal coefficients of selection calculated by the more exact method (on the basis of the means of the frequencies of melanics at different seasons) for the Kamenets-Podolsk, Kiev, Poltava, and Chernigov regions with the maximal coefficients of selection for the same regions calculated by the usual method (on the basis of mean annual frequencies of melanics).

An examination of table 6 leads to two conclusions. First, it is evident that the course of natural selection is very irregular both in the regions where the frequency of melanics showed a general increase during the investigated period

TABLE 6

A comparison of the maximal coefficients of natural selection of black hamsters calculated by the more exact and by the usual methods.

REGIONS	EXACT METHOD	USUAL METHOD
Kamenets-Podolsk	0.82	0.82
Kiev	0.76	0.74
Poltava	−1.39	−1.27
Chernigov	0.58	0.66

and in those where it showed a general decrease; not only is the intensity of selection different in different years in each region, but even its direction is frequently reversed. Secondly, the coefficients of natural selection are as a rule very high. In other words, the adaptive values of the alleles of usual coloration and of melanism are highly different, this difference being equally striking both when natural selection favors the former and when it favors the latter. Out of 43 cases where we could determine the minimal coefficients of selection, in only two cases the black mutation proved to be more or less neutral (Dniepropetrovsk region 1937–38 and Odessa region 1938–39). Typical are minimal coefficients of selection (both positive and negative) of the order 0.2–0.6 and maximal coefficients of selection of the order 0.7–0.9.

As has been shown above, a general increase in the frequency of black hamsters took place during the period of investigation on a large continuous territory, including several administrative regions of the Ukraine; a somewhat smaller area where the frequency of melanics showed a general decrease during the same period was also practically continuous. It is thus evident that a natural selection of black hamsters is at least partially controlled by some factors

operating over large territories. However, as we have already pointed out, there is good evidence for the existence of other factors of a more local type, as a result of the action of which the course of natural selection of melanics may considerably differ even in adjacent regions. In order to study this question we applied a method proposed by LIUBISHCHEV (1936) for a similar problem concerning the harm produced by insect pests. The coefficients of correlation between the minimal coefficients of selection of all pairs of adjacent regions[1] were determined for corresponding years during the period 1935–1938.

This coefficient of correlation proved to be only 0.25 ± 0.13, indicating that the role of local factors controlling the course of natural selection is very important. We further tried to ascertain whether such local factors operate in territories including several adjacent administrative districts or whether their

TABLE 7

Minimal coefficients of natural selection and correlation between them in pairs of adjacent districts.

PAIRS OF DISTRICTS	MINIMAL COEFFICIENTS OF SELECTION					COEFFICIENTS OF CORRELATION
	1934–35	1935–36	1936–37	1937–38	1938–39	
Kozelshchina	−0.48	−0.50	−0.25	0.76	No data	−0.82±0.17
Kobeliaki	−0.35	0.17	−0.27	0.51	No data	
Semenovka	0.70	−1.92	0.20	0.23	No data	0.98±0.01
Khorol	0.75	−3.96	0.15	−0.23	No data	
Malaya Devitsa	No data	0.24	0.35	0.29	0.04	0.03±0.45
Priluki	No data	0.77	−0.18	0.48	0.05	
Nosovka	No data	−0.09	−1.60	0.38	−0.08	0.46±0.39
Bobrovitsa	No data	0.78	0.11	0.29	0.28	
Volochisk	No data	0.53	−0.21	0.54	−0.28	0.97±0.03
Teofipol	No data	0.21	−1.04	0.57	−0.64	

action is restricted to still smaller territories. With this aim all pairs of adjacent districts were selected from which data were available for all the five years studied and where both the total number of hamsters trapped and the frequency of melanics were high enough to enable sufficiently exact calculations. Five pairs of districts answered these requirements—two in the Poltava region (Kozelshchina-Kobeliaki, Semenovka-Khorol), two in the Chernigov region (Malaya Devitsa-Priluki, Nosovka-Bobrovitsa) and one pair in the Kamenets-Podolsk region (Volochisk-Teofipol). For each pair of districts all four minimal coefficients of selection for the corresponding years were compared and their coefficient of correlation found (table 7).

As may be seen from table 7, the correlation between the coefficients of selection of adjacent districts is in three out of five cases positive, in one case

[1] These pairs are: Vinnitsa-Zhitomir; Vinnitsa-Kamenets-Podolsk; Vinnitsa-Kiev; Vinnitsa-Odessa; Dniepropetrovsk-Poltava; Dniepropetrovsk-Stalino; Dniepropetrovsk-Kharkov; Zhitomir-Kamenets-Podolsk; Zhitomir-Kiev; Kiev-Odessa; Kiev-Poltava; Kiev-Chernigov; Poltava-Sumy; Poltava-Kharkov; Poltava-Chernigov; Stalino-Kharkov; Sumy-Kharkov and Sumy-Chernigov.

negative, and in one case absent. The fact that in two cases the positive coefficients of correlation are statistically significant and very high makes it probable that the factors controlling the intensity of natural selection of melanics are in at least some cases common to adjacent regions—that is, to territories of the order of 800–1500 square kilometers.

NATURAL SELECTION OF MELANICS IN BASHKIRIA

The percentage of melanics in Bashkiria was relatively much more constant during the period 1937–1939 than in the Ukraine. The coefficients of selection were calculated here by the more accurate method (on the basis of the mean frequencies of melanics at different seasons), since the relative numbers of hamsters trapped during different seasons varied considerably in Bashkiria. These calculations showed that the general frequency of melanics in Bashkiria increased somewhat during the period 1937–1939, though the course of natural

TABLE 8

The frequency of black hamsters in 32 districts of Bashkiria in May-August 1933 and in May-August 1937.

PERIOD	TOTAL NUMBER OF HAMSTERS	NUMBER OF BLACK HAMSTERS	PERCENTAGE OF BLACK
May-August 1933	79765	23944	30.02
May-August 1937	71908	30637	42.61

selection was erratic. If we exclude the few districts in respect to which data were not available for all three years studied, the frequency of melanics in Bashkiria becomes 45.52 per cent in 1937, 45.12 per cent in 1938, and 50.89 per cent in 1939. The corresponding minimal coefficients of selection are −0.08 for 1937–38 and 0.18 for 1938–39. The minimal coefficients of selection for individual districts in the great majority of cases are also relatively low. The highest were observed in the Ufa district (0.31 for 1937–38 and −0.49 for 1938–39), but such high values are exceptional; in many districts they are too low to be significant. The greatest increase in the frequency of melanics during 1937–1939 took place in the Diurtulli, Kaltasy, Mishkino and Krasnousolsk districts, the first three of them being adjacent. A more or less considerable decrease in the frequency of melanics occurred only in one district (Kushnarenkovo).

Besides the data for 1937–39 there were available the data of the fur factories of "Soiuspushnina" concerning the frequency of black hamsters in Bashkiria in May-August 1933. Since the frequency of black hamsters is subject to considerable seasonal fluctuations, these data may be compared only with the data for the corresponding months of other years. Data on the frequency of melanics in Bashkiria in May–August, 1933, and for the corresponding months in 1937 are presented in table 8. Only 32 districts out of the 49 studied are taken into account.

Table 8 shows that the frequency of black hamsters in Bashkiria was in-

creasing not only in 1937–1939, but also during the preceding five years. The maximal coefficient of natural selection of melanics for these five years (1933–37) equals 0.58.

Out of 25 districts where melanics were present both in 1933 and 1937 their frequency increased significantly in 12 districts, remained more or less constant or slightly increased in ten districts, and significantly decreased in only three districts lying in the central part of Bashkiria (Iglino, Mishkino, and Ufa).

It is interesting to note that out of the four years (1933 and 1937–39) covered by this study of hamsters in Bashkiria, one year (1938) was a year of mass reproduction of hamsters (a "hamster year" according to the terminology of the fur-trade). This fact, which was pointed out by local trappers, was fully confirmed by the data on the numbers of hamster pelts purchased by the district factories during the corresponding years. The total number of hamster pelts purchased by the fur factories in Bashkiria in 1938 (548,075) is nearly double the number purchased in 1937 (253,050) or in 1939 (254,370). According to the observations of PETZCH (1936), in years of mass reproduction of hamsters a sharp increase in the frequency of melanics takes place. Our data on the positive correlation between the frequency of black hamsters and the density of the population of the species (GERSHENSON 1945) speak in favor of the same assumption. However, in the present case not only no increase in the frequency of melanics took place in Bashkiria, but the year 1938 showed even a slight decrease in the percentage of black hamsters. It is possible that this fact could be attributed to the climatic peculiarities of that year. The winter of 1937–1938 in Bashkiria was rather mild, and this could lead to the overwintering of unusually high numbers of hamsters. On the other hand, the summer of 1938 was exceedingly dry, and this could lead to a decrease in the frequency of melanics, the latter being better adapted to humid conditions (GERSHENSON 1945). In any case, it is clear that the conclusion reached by PETZCH is by no means universal, and in studying the connection between mass reproduction of hamsters and the frequency of melanics it is necessary to take into consideration the ecological peculiarities of the respective years.

SUMMARY

The data for the Poltava, Chernigov, Kamenets-Podolsk regions of the Ukrainian S.S.R. show that the relative frequencies of black hamsters in these regions undergo regular and significant changes from season to season. In winter the frequency of black hamsters in the Poltava region decreases, and in the Chernigov and Kamenets-Podolsk regions it increases. These changes in the frequencies of black hamsters during winter are caused by their lower (or, respectively, higher) viability compared to that of normal hamsters. The changes in the frequencies of black hamsters taking place during the summer months are less regular and less rapid than those taking place in winter, but, on the whole, these summer changes occur in directions opposite to the changes which take place in winter in the same region.

In Bashkiria the frequencies of black hamsters underwent increases during the winters of 1936–37 and 1938–39, but decreased in the winter of 1937–38. At

the end of every summer a sharp increase is observed, following which a sharp decrease takes place during autumn. Taken as a whole, the seasonal variations are smaller in Bashkiria than in the Ukraine.

Aside from the above cyclic changes in the frequencies of black hamsters, some systematic changes were taking place in the territories investigated during the period 1934–1939. In the western portion of the Ukraine the frequencies of black hamsters were increasing and in the eastern portion decreasing. The increase in the incidence of the melanics was accompanied by extension of their distribution area. It is very probable that a reduction of the distribution area of the melanics occurred in the eastern regions where their frequencies were diminishing.

The course of the natural selection of the melanics was very uneven both in those parts of the Ukraine where their general frequency was rising and where it was declining. The intensity of selection varied from year to year in each region, and reversals in the direction of selection occurred from time to time. This indicates that, besides factors which determine the general trends of natural selection in large territories, an important role is played by more local influences which control the course of selection in smaller subdivisions of these territories.

A general and fairly rapid, though uneven, rise in the frequencies of black hamsters took place in Bashkiria in 1933–1939.

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FURTHER DIVISION OF CONTRASTING ANTIGENS IN SPECIES HYBRIDS IN DUCKS[1]

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EVIDENCE for the existence of antigenic differences in the red blood cells of two species of ducks, Muscovy (*Cairina moschata*) and Mallard (*Anas Platyrhynchos platyrhynchos*), and their hybrid has been presented in a previous report (McGIBBON 1944). It was found that each species possessed antigens specific to itself as well as others common to both. The cells of the hybrids, except for individual differences, contained the major portion of the antigens present in the parental species and, in addition, a new or "hybrid" substance not found in either parent. By appropriate tests, the cells of the three kinds of ducks could be readily distinguished.

A segregation of what appeared to be a pair of contrasting antigens specific to Muscovy was noted among the hybrids from matings between Muscovy and Mallard. That is, the hybrids obtained from matings between a Muscovy male (P694) and Mallard females carried in their red blood cells one or the other of these two substances specific to Muscovy, called A1 and A2, respectively (McGIBBON 1944). As previously reported, 13 hybrids carred A1, and 12 had A2. The results of tests for the divisibility of each of these substances, as well as the distribution of the two characters A1 and A2, or parts of them, in the cells of other hybrids and Muscovies are given in this report.

MATERIALS AND METHODS

The cells of 71 hybrids resulting from reciprocal matings between Muscovies with Mallards were available for testing, as well as those of a number of Muscovies and Mallards.

The reagents used in this study were prepared from immune serum developed in ducks. The details of immunization have been given in a previous report, but briefly the procedure was as follows. Immune sera were produced following transfusions between hybrids from the Muscovy male, P694—blood from an A1 individual being injected into a sib possessing A2, and vice versa. Prior to the first transfusion, a sample of the recipient's serum was tested for normal antibodies. In the course of these experiments no agglutinative reactions were observed with the normal sera of 32 hybrids so tested. The immunization procedure consisted of giving seven intravenous injections of citrated whole blood during a four-week period. The immune sera from those ducks with satisfactory titers, determined by trial bleedings, were obtained on two

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consecutive days (between the third and sixth) following the last injection of cells.

Agglutinations were performed by adding to 0.1 cc of immune serum in varying dilutions (increasing by halves) one drop of a 2 percent saline suspension of washed red blood cells. These were made in small Pyrex tubes and were read after standing for two hours at room temperature and again after overnight storage in the icebox. For the absorptions, the immune serum was diluted according to its titer and mixed with a quantity of washed cells. The mixture was agitated gently at frequent intervals and kept at room temperature for 30–45 minutes. After centrifugation, the fluid was again mixed with another quantity of cells and allowed to stand for two hours. This was repeated until the test fluid no longer agglutinated the cells used in absorption.

RESULTS

On the assumption that the antigens A_1 and A_2 are contrasting genetic characters differentiating the hybrid offspring of the Muscovy male, P694, the immunization of a hybrid carrying A_2 in its cells with blood from a sib containing A_1 should result in the production of antibodies principally for the A_1 character. The reciprocal immunization would be expected to produce antibodies for the A_2 substance. It then should be possible, using reagents for each of these substances prepared from such antisera, to assay the cells of hybrids from various matings, as well as those of Muscovies, for the presence or absence of A_1 and A_2.

The immune sera produced following the transfusions of blood containing A_1 into sibs possessing the A_2 antigen have been called "anti-A_1." The reciprocal immunization yielded "anti-A_2" sera. The cells of many Mallards, as well as those of Muscovies and hybrids were reactive with these antisera, presumably by virtue of antigens *common* to the two species, but which were segregating in the hybrids. To obtain reagents for the A_1 or A_2 antigen, respectively, it was therefore necessary to absorb each immune serum with the cells of Mallard, thereby removing all agglutinins except those specific for either the A_1 or the A_2 character. This was accomplished by using in absorptions of the immune sera the cells of either a single Mallard or a pooled mixture from several birds. In each case all antibodies were always removed for the cells of all of 16 Mallards that were available for testing.

These two kinds of antisera, following absorptions by the cells of Mallard, provided reagents specific for the A_1 and A_2 cellular characters, respectively. The reagent for the A_1 substance reacted only with the hybrid cells classified as A_1 by the use of rabbit immune serum (McGibbon 1944). Likewise the reagent for A_2 recognized only the cells of those hybrids containing that antigen (A_2), as shown by previous tests with rabbit immune sera. Hence at least a portion of the antibody content must have been similar in the two kinds of immune sera, from rabbits and ducks, respectively.

For any immune serum in these experiments, the cells of two or more ducks were considered equivalent when each by absorption of that serum removed antibodies for the cells of the other(s). It would be expected that cells equiva-

TABLE 1

A summary of the results of tests showing the division of the A1 character in the cells of hybrids and Muscovies.

KIND OF INDIVIDUAL (AND MUSCOVY PARENT IF HYBRID)	CELLS OF	ANTIGENS PROPOSED	ANTI-A1 SERUM ABSORBED BY THE CELLS OF MALLARD IN COMBINATION WITH EACH OF THE FOLLOWING: (SERUM DILUTIONS 1:4 AND 1:8)																	
			—	122	739	740	1276	118	133	3585	A588	268	810	775	1276 +220	1276 +232	118 +232	133 +220	3585 +810
			a1:1* :2 :3 :4 :5	—	a1:1 :2 :3 :4 :5	—	a1:2 :3 :4 :5	a1:3 :4 :5	a1:4 :5	a1:5	—	a1:1 :2 :4 :5	a1:1 :2 :3 :4	—	a1:2 :3 :4	a1:2 :4 :5	a1:4 :5	a1:4	—
	Mallard	—	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Hybrid (♂P694)	122	A1:1, 2, 3, 4, 5	+	o	+	o	+	+	+	o[1]	o	+	+	o	—	+	±	+	o
Hybrid (♂P694)	739	—	o	o	o	—	o	o	o	o	—	o	o	o	—	—	—	—	—
Hybrid (♂P694)	740	A1:1, 2, 3, 4, 5	+	o	++	o	+	±	±	o[1]	o	—	—	o	—	—	—	—	o
Muscovy	1276	A1:1	+	o	++	o	o	o	o	o	o	+	+	o	o	o	o	o	—
Hybrid (♂P691)	118	A1:1, 2	+	o	±	o	+	o	o	o	o	±	+	o	+	+	o	o	—
Muscovy	133	A1:1, 2, 3	+	—	+	—	+	+	o	o	o	+	+	o	+	+	o	o	o
Muscovy	3585	A1:1, 2, 3, 4	+	o	++	o	+	+	+	o	o	+	+	o	+	+	+	+	o
Muscovy	A588	A1:1, 2, 3, 4, 5	+	o	++	o	+	+	+	+	o	++	+	o	—	+	—	—	o
Hybrid (♀A587)	268	A1:3	+	—	±	—	+	+	o	o	—	o	±	—	—	o	o	o	o
Hybrid (♀A596)	810	A1:5	+	—	±	o	+	+	+	+	—	±	o	o	o	+	+	o	o
Hybrid (♀A596)	775	A1:1, 2, 3, 4, 5	+	o	—	o	+	+	+	+	o	+	+	o	—	+	—	+	o
Column:	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

Symbols: ++=strong agglutination, +=definite agglutination, ±=definite agglutination though clumps smaller, o=no agglutination; at the first (absorbing) dilution of the antiserum. A dash (—) indicates that the absorption or combination was not made.

* Proposed agglutinins present in the serum.

[1] Discrepant interactions, see text.

lent in antigenic content should give parallel reactions when tested with other reagents. Also, the reagents prepared by using such cells in separate absorptions should give similar reactions (presence or absence of agglutination) with all other cells. The cells which did not fulfill these requirements have been considered unequal in antigenic content. There were also a few inconsistencies encountered, and these have been treated as discrepant reactions.

For brevity, the results of the detailed experiments have been omitted which established (1) the equivalence and (2) the dissimilarity of antigenic composition, by virtue of cross agglutination tests involving the cells of individuals belonging to the same or to different immunologically distinct groups, respectively, but these will be supplied on request.

Fractionation of the A1 substance

A summary of the results of numerous tests using the cells of selected hybrids and Muscovies with the reagent for the A1 character and with various testfluids derived from this reagent is presented in table 1. The cells of Mallard as well as those of the particular individual (hybrid or Muscovy) used in the absorption were always included in the tests of the reagent and fluids obtained from it. These served as controls for the completeness of absorption—that is, the lack of agglutination of such cells showed that the antibodies for them were removed. For the positive control, the cells of the hybrid which served as the donor in immunization (or sibs identical with it) were always tested with each reagent.

In the fourth column of table 1 are given the reactions of the cells of various Muscovies and of hybrids from different matings with the reagent for the A1 antigen (anti-A1 serum absorbed by Mallard cells). All these cells listed were agglutinated, except those of hybrid 739 which was one of the 13 hybrid offspring of the Muscovy male, P694, which carried the A2 character.

However, differences in the capacities of these *reactive* cells to absorb the antibodies from this reagent were noted. For example, the cells of all hybrids of P694 (13 tested) removed antibodies from the reagent for A1, not only for themselves but for all other cells tested. The cells of hybrids 122 and 740 listed in the table and the reagents produced by their use in absorptions (see columns 5 and 7) are typical of all others in this family carrying A1 in that they removed all the antibodies from the reagent for A1. On the other hand, it may be seen from the results given in the table (column 6) that further exhaustion of the A1 reagent by the cells of the hybrids containing A2 (bird 739) caused no appreciable change in reactivity towards cells agglutinated by the A1 reagent (compare reactions in columns 4 and 6). Up to this point, both the genetic and immunological results coincide in the conclusion that the segregation of A1 and A2 in the hybrid family could be explained by assuming that A1 and A2 were contrasting antigens produced by allelic genes.

But when a reagent, prepared by using in absorption the reactive cells of a Muscovy (1276) in combination with those of Mallard, was tested with the cells presumably carrying A1 (column 8), all the cells except those used in absorption were still agglutinated. Since the cells of 1276 definitely contained at

least a part of the A1 antigen (they were reactive with the A1 reagent, see columns 4 and 6) but by absorption removed antibodies only for themselves, it is clear that only a part of the A1 substance was contained in these cells. This fraction has been called A1:1.

Furthermore, each of the testfluids obtained by absorbing the reagent for A1 separately with the cells of the hybrid 118 and the Muscovies 133, 3585, and A588 reacted differently (see columns 9–12) with cells which were reactive with the non-fractionated reagent for A1. That is, the testfluid obtained following exhaustion by the cells of hybrid 118 lacked antibodies only for antigen A1:1 (Muscovy #1276) and for those of 118 but agglutinated all others (column 9). However, since these cells of 118 were agglutinated by the reagent from which the antibody for A1:1 was removed (column 8), the logical inference follows that the cells of 118 possessed antigen A1:1, plus at least one other. This additional part of the A1 complex has been called A1:2, and the cells of 118 thus contained A1:1, 2. Further, since exhaustion of the A1 reagent by the cells of Muscovy 133 removed antibodies only for A1:1, 2 (118) and the absorbing cells (column 10), and because the cells of 133 were still reactive when antibodies for A1:1, 2 were absent (column 9), another part called A1:3 must be proposed for the cells of 133, so the antigens present in these cells of Muscovy 133 comprised A1:1, 2, 3. In like manner, a comparison of the interactions between the testfluid resulting from using the cells of Muscovy 3585 in absorption of the reagent for A1 (column 11) on the one hand and those involving the reagent lacking antibodies for A1:1,2,3 (column 10) with the cells of these Muscovies (133 and 3585) indicates that the Muscovy 3585 possessed not only A1:1,2,3 (133) but another fraction as well, called A1:4. Similarly, a comparison of the interactions between all cells tested and the fluids obtained by absorbing the reagent for A1 separately with the cells of Muscovy 3585 and A588 (columns 11 and 12, table 1) illustrates that the Muscovy A588 possessed another fraction, not present in the cells of 3585, which has been called A1:5. The cells of A588 thus contained A1:1, 2, 3, 4, 5 and were equivalent (as shown by reciprocal absorption tests) to all A1 cells of hybrids, not only from the families represented by 122 and 740 and by 775 in the table, but to those containing A1 from two other families as well.

Incompatible interactions between the cells of 122 or 740 on the one hand, and on the other, those of 775 when these latter were mixed with the testfluid obtained by absorbing the A1 reagent with the cells of 3585 will be noted (see column 11). These cells (122, 740, and 775) as well as those of 34 other hybrids (not listed in the table) had each been shown, by reciprocal absorption tests, to be identical in antigenic content. Antibodies for A1:5 should be present in this reagent (for 3585) and should react with all cells containing this part of the A1 complex. No explanation can be suggested to account for the lack of agglutination on repeated tests of this reagent (column 11) with the cells of 122 (homologous) or 740 as well as with those of the several other sibs from the family of P694. The presumably equivalent cells of hybrids from three other families, represented by those of 775 in the table, were without exception always agglutinated by this reagent.

The reactions with the cells of hybrids 268 and 810 listed in table 1 are representative of two other groups of antigenic complexes encountered in this study. While both were reactive with the A1 reagent (column 4), nevertheless when used in absorption of this reagent each removed antibodies only for its own (columns 13 and 14) and equivalent cells. This, together with the observation that the cells of 268 were reactive with the testfluids obtained following absorption with the cells of 1276 (A1:1) or 118 (A1:1, 2) (columns 8 and 9), but not when the cells of 133 (A1:1, 2, 3) or 3585 (A1:1, 2, 3, 4) (columns 10 and 11) were used, indicated that the cells of hybrid 268 contained the A1:3 fraction, and possibly A1:2 as well. However, the observed agglutination of the cells of 118 (A1:1, 2) with the fluid resulting by absorption of the A1 reagent with the cells of *both* 1276 (containing A1:1) and 232 (equivalent to hybrid 268 in other tests tests and carrying A1:3), as shown in column 17 of table 1, excluded the possibility that the cells of 268 contained A1:2. Following the combination of the cells of 268 (having antigen A1:3) with those of the hybrid 118 (having antigen A1:1, 2) in absorption (column 18), the resulting fluid failed to agglutinate the cells of 133 (with A1:1, 2, 3), thus substantiating the conclusion that the cells of the hybrid 268 contained only A1:3. In exactly the same manner the hybrid 810 and ducks identical with it have been shown to possess only the A1:5 fraction of the A1 complex in their cells; the pertinent tests for this statement are given in columns 16, 19 and 20 of table 1.

The respective fractions of the A1 antigen contained in the different cells listed in table 1 are given in column 3. In all, seven different combinations (namely, A1:1, A1:3, A1:5, A1:1, 2, A1:1, 2, 3, A1:1, 2, 3, 4 and A1:1, 2, 3, 4, 5) of one or more of the five parts of this character were encountered in this study. Whether or not other combinations would be found in other birds cannot be stated at present, nor can it be stated that A1:2 or A1:4 may or may not occur alone.

Fractionation of the A2 substance

Evidence for a division of the A2 character has also been obtained as the result of tests analogous with those concerning the A1 substance as presented above. Several anti-A2 sera were produced following transfusions of blood from A2 hybrids into sibs possessing A1, and the absorption by cells of Mallard removed from these antisera all antibodies except those for A2. This analysis was somewhat more tedious than with anti-A1 sera, since the reactions with A2 cells were generally weaker in expression even though there was little difference in titer.

The A2 reagent agglutinated the cells of many hybrids and Muscovies, indicating that this character was present in all such reactive cells, but it did not react with cells of any hybrids containing A1 in the family from Muscovy P694. These reactions are listed in column 4, table 2. Furthermore, the reactive cells differed in their ability to remove antibodies when used in absorption of the A2 reagent, thereby implying different fractions of the A2 substance, exactly as was done with the A1 complex. The reactive cells of the hybrids 117 and 739 (as well as those of seven other sibs identical with these but not listed in

the table) from the Muscovy male, P694, when used in absorption of this reagent, removed agglutinins not only for themselves but for all cells tested (columns 5 and 6). Such cells presumably therefore possessed the A2 character *in toto*.

The cells of the hybrid 810 were definitely agglutinated only by the A2 reagent prepared from the first anti-A2 serum produced, and but faintly or not at all by two others obtained later. Hence, two kinds of interaction are recorded

TABLE 2

A summary of the results of tests showing the division of the A2 character in the cells of hybrids and Muscovies.

KIND OF INDIVIDUAL AND MUSCOVY PARENT, IF HYBRID	CELLS OF	PROPOSED ANTIGENS IN CELLS	ANTI-A2 SERUM ABSORBED BY THE CELLS OF MALLARD IN COMBINATION WITH EACH OF THE FOLLOWING: (SERUM DILUTION 1:4)								
			— a2:2 :3 :4	117 —	739 —	810 a2:2 :3 :4	118 a2:3 :4	268 a2:2 :4	133 a2:4	1276 a2:3	A588 —
—	Mallard	—	o	o	o	o	o	o	o	o	o
Hybrid (♂P694)	117	A2:2, 3, 4	±	o	o	±	±	−	±	−	o
Hybrid (♂P694)	122	—	o	−	o	o	o	−	o	−	o
Hybrid (♂P694)	739	A2:2, 3, 4	+	o	o	±	−	±	±	±	o
Hybrid (♀A596)	810	—?	±, o[1]	o	−	o	o	o	o	o	o
Hybrid (♂P691)	118	A2:2	±	o	−	±	o	±	o	o	o
Hybrid (♀A587)	268	A2:3	±	−	−	±	±	o	o	−	o
Muscovy	133	A2:2, 3	+	−	−	++	±	+	o	±	o
Muscovy	1276	A2:2, 4	±	−	o	−	+	+	±[2],(o)	o	o
Muscovy	A588	A2:2, 3, 4	±	o	−	++	+	+	±	±	o
Column	2	3	4	5	6	7	8	9	10	11	12

For explanation of symbols, see table 1.

[1] These cells reacted differently with different antisera; see text.

[2] The lack of agglutination noted on one occasion most probably was a discrepancy; see text.

for these cells in column 4. However, when the cells of 810 were used to absorb the particular A2 reagent with which they were reactive, antibodies were removed only for themselves while those of all other ducks were agglutinated, as shown in column 7, table 2. This finding indicated that the cells of 810 possessed only a fraction of the A2 character because of their inability to absorb all antibodies from the reagent for A2—a result quite in contrast with that noted when the cells of hybrids 117 or 739 which possessed A2 *in toto* were used (see columns 5 and 6). This fraction, possessed by 810, has been designated A2:1.

Since the quantity of anti-A2 serum which yielded the A2 reagent containing the antibody specific to the A2:1 component was limited and soon became exhausted, it was not possible in the tests with the cells of the hybrids and Muscovies which follow, using an A2 reagent which lacked the antibody for A2:1,

to assay these cells for the presence or absence of this component. Hence, this probable fraction of the A2 antigen will not be considered further. One should bear in mind, however, that the lack of agglutination shown for the cells of 810 with the testfluids listed in columns 4, 8, 9, 10, 11 and 12 means only that the antibody for A2:1 was absent and not that the cells used in absorption necessarily possessed the antigenic component and thereby removed it. The non-reactivity shown in column 4 for the cells of 810 indicated that the antibody detecting the antigenic component A2:1 was not present in the particular A2 reagent used.

When the reactive cells of the hybrid 118 were used to absorb the A2 reagent, they removed antibodies only for themselves but not for any others (column 8). This indicated that the cells of 118, though reactive with the reagent for A2, nevertheless possessed only a fraction of this complex, which has been called A2:2. Similarly, the cells of another hybrid, 268, though agglutinated by the A2 reagent (column 4), did not by absorption of it remove antibodies for the cells of any other hybrid or Muscovy except its own. Therefore, it appears logical to propose that the cells of 268 contained only a fraction of the A2 complex, but a different one than that possessed by hybrid 118 (A2:2). This component in the cells of hybrid 268 has been termed A2:3.

Also, when the A2 reagent was absorbed by the reactive cells of the Muscovy 133 (column 10), antibodies were removed for these cells as well as for antigens A2:2 (hybrid 118) and A2:3 (hybrid 268) but not for cells of other ducks, as hybrid 117 or Muscovy 1276. The interactions observed with this testfluid indicated not only that the Muscovy 133 possessed both the A2:2 and A2:3 components, but also that at least one other part of the A2 complex must have been present in the cells of 117 and 1276 to account for their reactivity with this testfluid. This part of A2, different from A2:2 and A2:3, which was carried in the cells of the Muscovy 1276 as well as in those of hybrids 117 and equivalent ones, has been called A2:4.

Absorption of the reagent for A2 by the cells of Muscovy 1276 removed antibodies for the A2:2 component (118) as shown in column 11, indicating that the cells of 1276 contained the A2:2 fraction in addition to A2:4 as shown above. The lack of agglutination observed for the cells of 1276 on one occasion when mixed with the testfluid resulting by exhaustion of the A2 reagent with cells of 133 (column 10) can justifiably be considered a discrepancy, since these cells were definitely agglutinated in many other tests with this testfluid performed both before and after this apparent error was recorded. And, finally, the cells of the Muscovy A588, when employed in absorption of the A2 reagent, removed antibodies for all cells tested (column 12), including those of hybrids, 117 or 739, which possessed A2 *in toto*, thus furnishing evidence that this Muscovy (A588) likewise possessed all parts of the A2 complex. In fact, only three Muscovies (A588 and two others) out of over 100 tested possessed all parts of the A2 character.

Thus the A2 antigen has been shown to be divisible into at least three, probably four, parts. The five combinations (namely, A2:2, A2:3; A2:2, 3; A2:2, 4, and A2:2, 3, 4) consisting of one or more of the three parts of this substance

encountered among different individuals (hybrids and Muscovies), listed in table 2, may be seen in column 3. The antigenic fraction A2:1 possessed by the hybrid 810 is not given, since it was not possible to test the cells of all the ducks listed for the presence or absence of this fraction, as pointed out previously.

Combinations of parts of A1 and A2 in the cells of hybrids and Muscovies

Of a total of 71 hybrids which resulted from matings between seven Muscovies and Mallards whose cells were tested with both the A1 and A2 reagents, the reactive cells of 62 have been used in absorptions of either the A1 or A2 reagent, or both. The other nine hybrids were not available for the absorption tests. As a result of these absorptions and the reactivities of the cells of these 62 hybrids with the various testfluids, it was possible to assign to each hybrid the part or parts of the A1 or A2 complexes which they contained. These are given in table 3, along with the proposed complexes of their respective Muscovy parents. It may be seen that 37 hybrids from four families possessed A1:1, 2, 3, 4, 5 in their cells, 13 other hybrids from three matings carried A2:2, 3, 4, and six from two families contained A1:5 in their corpuscles.

In addition, as shown in table 3, there were also two hybrids in one family whose cells possessed the antigenic combination A1:1, 2–A2:2, and four from another with A1:3–A2:3 in their corpuscles. The recognition of these two antigenic combinations, displayed by species hybrids from different Muscovy parents, is noteworthy since it illustrates that portions of each of the two "contrasting" characters specific to Muscovy may be carried by individual hybrids. Since the species hybrids carry the genes for these species-specific substances presumably in the simplex state, it would be expected that comparable antigenic patterns would be encountered among Muscovies, as was indeed found to be the case. The genetic implications of this finding will be discussed later.

In all, the cells of 128 Muscovies have been tested with the reagents for A1 and A2. It was found that 47 of these possessed at least one part of the A1 antigen, 80 contained one or more parts of both A1 and A2, and a single Muscovy probably carried only components of the A2 antigen in its cells. The reactive cells of a number of these Muscovies have been used in absorptions of the two reagents. These included the parents of the species hybrids and a few others. As a result of these absorption tests, there are listed in table 3 the antigenic fractions of each complex that were present in the cells of the Muscovy parents of the species hybrids. And as a consequence of the segregation of the parts of these characters observed among the hybrids from each mating, or the antigenic pattern if all hybrids were identical, the different combinations of the antigenic parts transmitted as units are indicated for each parent as the numerator and denominator of a fraction, with the assumption that the genotypes and phenotypes are the same. For example, the species hybrids from Muscovy A587 possessed either the A1 complex *in toto* or A1:3–A2:3. Thus the antigenic components of A587 were undoubtedly $\frac{\text{A1:1, 2, 3, 4, 5}}{\text{A1:3–A2:3}}$, as is given in the table.

Certain Muscovies which had produced species hybrids when mated with Mallards were also mated *inter se*. The antigenic patterns of the cells of the resulting progeny were in reality a further check on the accuracy of those assigned to the hybrids, as listed in table 3. Five of the seven Muscovies which produced species hybrids were used in such matings. As an example, the cellular patterns of the progeny obtained from one of these matings together with those of the parents were as follows:

A587 ♀	×	P691 ♂
A1:1, 2, 3, 4, 5		A1:1, 2, 3, 4, 5
A1:3–A2:3		A1:1, 2–A2:2

Three offspring

133 ♂	134 ♀[2]	135 ♀
A1:1, 2–A2:2	A1:1, 2, 3, 4, 5	A1:1, 2, 3, 4, 5
A1:3–A2:3	A1:?	A1:3–A2:3

Assuming that the same kinds of gametes were produced as when each parent (Muscovy) was mated with Mallard (see table 3), the cellular patterns of the three offspring from this mating represent three of the four combinations anticipated from the result of tests with the cells of the species hybrids from each parent (disregarding crossing over, if linked genes were involved). That is, one may propose that the cellular pattern of Muscovy 133 resulted when a chromosome responsible for the fractions A1:3 and A2:3 was contributed by the parent A587 and another homologue for the characters A1:1, 2 and A2:2 by the male P691. Similarly, the antigens found in the cells of the two sibs may be explained.

Other matings were also designed, which included each of the three Muscovy offspring mentioned above as one parent, with the idea of observing further the transmission of these antigenic components as groups and to detect, if possible, any further subdivision of the immunological units, as A2:2, etc. Tests with the cells of the resulting progenies, however, failed to yield evidence either for further subdivision of any of the immunological fractions as identified in these experiments, or for the splitting up of any combination of these units which were not also noted among the species hybrids. In addition, Muscovies were also obtained from certain of these matings whose cellular patterns were identical with several of the combinations encountered among the hybrids. Among others, for example, Muscovies were obtained whose cells contained only A1:5 as well as others with A1:3–A2:3 which were identical with the corpuscles of hybrids 810 and 268, respectively. These findings indicate that within the Muscovy species, alleles with other effects, either not

[2] This duck probably was homozygous for the gene(*s*) controlling A1 *in toto*, since absorption tests involving the cells of a number of the progeny obtained by mating this individual with a sib (133) indicated that each of the offspring possessed all parts of the A1 antigen.

detectable with the reagents developed or recessive in nature, must also exist. If this be granted, one should then expect to find some individuals in an adequate sample of Muscovies whose cells would carry none of the eight known components of A1 and A2, as identified in this study and which in part differentiated the corpuscles of Muscovy from those of Mallard.

TABLE 3

Components of the A1 and A2 antigens possessed by Muscovies and their species hybrids obtained from matings with Mallard.

MUSCOVY PARENT	ANTIGENIC PATTERN OF MUSCOVY PARENT	NUMBER OF HYBRIDS FROM EACH FAMILY TESTED WITH REAGENTS A1 AND A2	PARTS OF A1 AND A2 CARRIED BY HYBRIDS WHOSE REACTIVE CELLS WERE USED IN ABSORPTION OF THE REAGENTS; NUMBER OF EACH TYPE IN PARENTHESES	
♀ A587	A1:1, 2, 3, 4, 5 / A1:3–A2:3	7	(3) A1:1, 2, 3, 4, 5;	(4) A1:3–A2:3
♀ A588	A1:1, 2, 3, 4, 5 / A2:2, 3, 4	10	(7) A1:1, 2, 3, 4, 5;	(3) A2:2, 3, 4
♀ A596	A1:1, 2, 3, 4, 5 / A1:5	21[3]	(14) A1:1, 2, 3, 4, 5;	(6) A1:5
♀ A704	A1:1, 2, 3, 4, 5 / A1:5			
♀ A705[1]	A2:2, 3, 4 / A1:?	1	(1) A2:2, 3, 4	
♂ P691	A1:1, 2, 3, 4, 5 / A1:1, 2–A2:2	2	(2) A1:1, 2–A2:2	
♂ P694[2]	A1:1, 2, 3, 4, 5 / A2:2, 3, 4	30[4]	(13) A1:1, 2, 3, 4, 5	(9) A2:2, 3, 4

[1] These cells were not used in absorption of the reagent for A1; hence it is not known what part, or parts, of this complex (if any) were present.

[2] Probable pattern, based on tests with the progeny, since these cells were not available for absorption tests.

[3] The cells of one hybrid were not available for the tests for various fractions of A1.

[4] The cells of eight hybrids from this family were not available for the absorption tests of these, four were reactive only with the A1 reagent, and an equal number were agglutinated only by the reagent for the A2 antigen.

The presence in the cells of the species hybrids of one or more fractions of the A1 and/or A2 antigens was, without exception, always associated with the possession of the same part or parts of either antigen by the Muscovy parent of the hybrids. And furthermore, no Muscovy was noted among those whose parentage was known which possessed a part of either complex that

was not also carried by one or both of its parents. Such findings can be reconciled only with the assumption that the parts of each antigenic complex A1 and A2 were under gene control.

DISCUSSION

In this paper are summarized the results of experiments that indicated a fractionation of the A1 and A2 antigenic complexes, specific to Muscovy, which seemingly were transmitted as contrasting unit characters in one family of species hybrids (Muscovy ♂ × Mallard ♀ ♀). The A1 character was shown to consist of at least five parts termed A1:1, 2, 3, 4, 5, while the A2 substance was subdivided into a minimum of three, probably four components, represented as A2:(1), 2, 3, 4. These fractions were found in various combinations, but not all the possible combinations were observed. The multiple nature of each of these characters, A1 and A2, was revealed as a consequence of assays of the cells of a number of Muscovies as well as of those of the species hybrids obtained from several of these Muscovies, following matings with Mallard. Either of two genetic explanations, both equally plausible in the light of the present evidence, may account for these findings.

One interpretation would assume that the parts of the "contrasting" complexes A1 and A2 in Muscovy were controlled by linked genes. Fairly close linkage is suggested by the finding that of 41 species hybrids from two Muscovies possessing all of both antigens, the cells of 33 hybrids definitely contained either all of A1 or all of A2; no hybrids of these familes were noted having in their corpuscles all of one complex and at least one part of the other. The cells of the other eight hybrids from these families were not available for the absorption tests, by which the possible fractionation of these antigens could be measured. It would seem reasonable, however, to propose that at least certain parts of A1 were controlled by genes allelic with others producing components of the A2 character. Although the particular alleles were not identified in this study, the combinations of the parts of each complex occurring in hybrids, such as A1:1, 2–A2:2 possessed by 118 or A1:3–A2:3 in the cells of 268, would eliminate allelic relationship of the genes for these parts, but only for these, there still being several other arrangements remaining as possibilities.

However, in addition to this occurrence of A1:1, 2–A2:2 or A1:3–A2:3 in the cells of hybrids, the presence of only A1:5 in the corpuscles of certain hybrids from Muscovies A596 and A704 was also noted. These findings, as well as the recognition of Muscovies each having cellular patterns identical with the last two groups of hybrids mentioned (A1:3–A2:3 and A1:5), force the assumption under this explanation that alleles with effects other than those identified must also exist in the Muscovy species. Then, crossing over within the species between such genes and those for parts of A1 and A2 with subsequent linkage would account for the combination of parts of these encountered in this study.

The explanation involving linked genes controlling the components of the A1 and A2 antigenic complexes in the Muscovy species is somewhat analogous

to a situation reported by DUNN and CASPARI (1942) in the mouse. These authors proposed that five mutations with similar effects on the tail region involve three adjacent loci.

An alternative explanation, equally logical for the data presented, would be that a series of alleles at a single locus on a Muscovy chromosome produced each of the components, or combinations of components, of A1 and A2. This explanation also seems justified since not more than two classes of cells were found among the species hybrids from any mating nor were more than four observed among the Muscovy progeny. Thus one would anticipate different alleles at a locus to produce A1:1, 2, 3, 4, 5; A1:5; A2:2, 3, 4; A1:1, 2–A2:2 or A1:3–A2:3 as encountered in the cells of species hybrids dealt with in this study.

It is possible, although somewhat improbable, that one of a series of alleles could alone produce parts of otherwise *contrasting* characters. Such an explanation would be required to account for the presence in a single hybrid individual of the combination A1:3–A2:3 observed in hybrid 268 or A1:1, 2–A2:2, noted in 118. Furthermore, alleles for the five combinations of the parts of A1 and A2 noted in the cells of the hybrids, together with one having no discernible effect, may account for the cellular patterns exhibited by all the Muscovies dealt with in this study, except two, 3585 (A1:1, 2, 3, 4) and 1276 (A1:1–A2:2, 4) from which no hybrid progeny were obtained.

The combinations of the parts of the A1 and A2 complexes encountered in the cells of the hybrids are conceivable, however, if a series of mutations at a locus on a pair of Muscovy chromosomes had successively affected different fractions or reactive groups of the antigen, each fraction thereby first becoming detectable when contrasted with its absence, to the ultimate lack of any antigenic activity whatsoever. Or contrariwise, similar results would obtain if mutations at a locus had successively added reactive groups to a substance which was initially without antigenic activity.

A situation, similar to that presented here, has been reported by STORMONT, IRWIN, and OWEN (1945) for a number of cellular antigens in cattle. These authors have proposed that at least three antigens (B, G and K) are produced either by an allelic series or by linked genes, one for the absence of all three, one for antigen B, one for G, one for B and G together, and one for the BGK complex.

An explanation involving multiple alleles controlling different antigenic combinations has also been recently proposed by WIENER (1943) to account for the variants of the *Rh* blood type observed in the red blood cells of humans.

Whether the parts of the A1 and A2 complexes are controlled by linked genes or by members of an allelic series cannot be stated at present. Nevertheless it is noteworthy that only relatively few components of either complex—namely, A1:1, A1:3, A1:5, A2:2 and A2:3—have been detected separately in the cells of individual hybrids or Muscovies. Apart from the errors of sampling, the possibility that the other conceivable combinations of parts of the A1 antigen, for example, might be encountered would depend on the mode of inheritance of the parts and whether a fraction as A1:1, A1:3, or A1:5 would

be a prerequisite for the occurrence of other components as A1:2 or A1:4 in a single duck. The detection of A1:1, 2, 3, 4, 5; A1:1, 2, 3, 4; A1:1, 2, 3; A1:1, 2; A1:1; A1:3; or A1:5 in the cells of different individuals bears somewhat of a resemblance to the step-like effects of the scute alleles on bristle reduction in Drosophila (quoted by WADDINGTON 1939). In both instances the step-like relationship noted between phenotypes is not understood, although the latter has been considered a developmental phenomenon by STURTEVANT and SCHULTZ (1931).

SUMMARY

Further study with what at first appeared to be a pair of contrasting cellular characters specific to Muscovy, not shared with Mallard, has shown that each was composed of several parts. One was found to consist of at least five components and the other a minimum of three, probably four parts.

Different combinations of the parts of the two characters were encountered in the red blood cells of the species hybrids and also in Muscovies.

Either of two genetic explanations seem logical for an interpretation of the data obtained. One involves linked genes on a single pair of Muscovy chromosomes controlling each of the parts of the two characters, with certain ones probably allelic. The other proposes that a series of alleles at a single locus on a Muscovy chromosome control the expression of each of the components, or combinations of components, of the two complexes.

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ON THE BIOLOGY AND GENETICS OF SCAPTOMYZA GRAMINUM FALLEN (DIPTERA, DROSOPHILIDAE)

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IN THE spring of 1942 genetic work was begun on three Drosophilidae: *Scaptomyza graminum*, *S. adusta*, and *Chymomyza amoena*. The purpose of this work was to make a comparison between the genetic chromosomes of Drosophila and those of some other Drosophilidae. Of the three species chosen, *C. amoena* soon proved itself unsatisfactory as a laboratory animal, partly because of the habit of the adults of constantly waving their wings as they moved about the culture bottle, with the result that they got stuck if the bottle or the food was at all moist. Both species of Scaptomyza could be cultured, but since it was difficult to secure large numbers of wild *S. adusta*, most of the work was done on *S. graminum*. Strains from the Rochester, N. Y., and St. Louis, Missouri, areas were studied, and large numbers of mutations were found, both in the progeny of the wild flies and as spontaneous occurrences in the laboratory. In 1943 all the laboratory stocks became infected with bacteria which made stock-keeping too difficult to warrant continuing the work.

Since practically nothing is known about the genetics of any Drosophilidae other than Drosophila, it is felt that a description of the mutants discovered, as well as an account of some of the peculiarities of *S. graminum*, may have comparative value even though this account is of necessity somewhat fragmentary.

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TAXONOMY AND MORPHOLOGY

Scaptomyza graminum was described by FALLEN in 1823. This species, like others in the genus, looks enough like Drosophila so that the casual observer might be confused. STURTEVANT (1921) lists Scaptomyza as one of the twenty-two genera in the family Drosophilidae, and gives the following brief description of the genus.

> Very close to Drosophila, but differs in the following respects: two or four acrostichal rows of hairs in front of the transverse suture (six or more in Drosophila), two rows between the dorsocentral bristles (four or more in Drosophila): thorax, abdomen, and wings more slender, prescutellars never present.

The same author (1942) suggests that Scaptomyza is closely related to the subgenera Drosophila and Sophophora of the genus Drosophila.

[1] The work reported herein was started while the author held the position of Research Assistant to DR. CURT STERN, Department of Zoology, UNIVERSITY OF ROCHESTER. Part of the cost of the work was defrayed by a grant from the ST. LOUIS ACADEMY OF SCIENCE.

FALLEN'S 1823 description of *S. graminum* is very brief, and a more complete description of the imagines is given below. This description is based on living material from the St. Louis region.

Male: Arista with about seven branches. Antenna brownish-yellow. Front velvety golden-brown. Triangle and orbits pollinose grayish-yellow, lighter anteriorly. Middle orbital one-fourth the length of the anterior. Anterior orbital three-quarters the length of the posterior. Second oral less than one-third the length of the first. Palpi pale yellow with several hairs; one prominent bristle at the tip. Carina prominent and nose-like. Face and cheeks silvery. Occiput rather dark gray. The greatest width of the cheeks one-seventh the greatest diameter of the eye. Eyes with thin, blond pile.

Acrostichal hairs in two rows. Dorsocentral and scutellar bristles strong, anterior scutellars divergent. Two pollinose grayish-brown longitudinal stripes on the mesonotum extending medially to the acrostichal rows, and laterally to the first row of hairs outside of the dorsocentral rows. The mesonotum lateral to and between these stripes dull, yellowish-brown. Scutellum pollinose grayish-brown. Pleurae light brownish-yellow, legs yellow, becoming darker toward tips. Sternoindex about 0.4.

Abdomen shining, with wide light-brown abdominal bands on the anterior side of each segment. These bands are widely interruped medially in the anterior segments, less so in the posterior segments, and not at all in the last segment. The bands become darker and broader as they progress posteriorly, the last segment being almost black. Space not covered by bands light shining yellow.

Wings clear, veins gray. Costal index about 3.2; 4th vein index about 1.5; 4c index about 0.7; 5x index about 1.4.

Body length about 2¼ mm. Wing length about 2 mm.

Female: As in male except: abdomen lighter colored, first three segments frequently without abdominal bands, last segment with band which may or may not be interruped, but is never as dark as the last abdominal band in the male.

Body length about 2½ mm. Wing length about 2¼ mm.

Young flies captured in early spring are as a rule very dark in color, while those captured in June or July are always much lighter. That this difference in color is at least partially dependent on the temperature at which development occurs has been demonstrated by raising strains in the laboratory at different temperatures. Thus, flies raised at 26°C are light yellow when they emerge, becoming darker as they age, while those raised at 16°C emerge almost black. The colors mentioned in the description above apply to flies raised at 25°C in the laboratory and aged for about a week. Many flies captured in nature would be darker or lighter, depending on the season and age of the flies.

PATTERSON (1943) figures the male and female internal genitalia, the pupa case, and the eggs of this species, and gives the following notes on the genitalia.

The inner testes are large and not coiled, and of a deep yellow color; the outer testes consist of one and one-half coils or gyres, which are light yellow in color. The ejaculatory sac has a pair of branched diverticula. The spermathecae are spherical and chitinized. Ventral receptacle is a small tangled mass, not definitely coiled.

The egg has two short, thick filaments, and the pupal-horns are very short. PATTERSON gives the pupal-horn index as 17.6. In the New York and Missouri material it is approximately 16.5.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

Scaptomyza graminum is widespread in its distribution. It is recorded from the Faroe, Canary and Madiera Islands, from many parts of Europe, from

Egypt, and from Formosa. In North America it has been collected in most of the eastern United States and in some of the western states. The following list of states and provinces in which it has been collected is extracted from STURTEVANT (1921), FROST (1923), MALLOCH and MCATEE (1924), and PATTERSON (1943). The list follows: Vermont, Massachusetts, New York, New Jersey, Ohio, Maryland, District of Columbia, Virginia, West Virginia, South Carolina, Tennessee, Georgia, Florida, Alabama, Louisiana, Illinois, Wisconsin, Minnesota, Kansas, Texas, New Mexico, Arizona, Idaho, Washington, and British Columbia. The author has collected or identified specimens from Ohio, Illinois, New York, and Florida (in the above list) and can add to the list Pennsylvania, Michigan, Missouri, and Ontario, Canada.

Scaptomyza graminum is one of the leaf-mining diptera. FROST (1923) reports that the larva mines the leaves of the following plants in North America: *Petasites officionalis* (coltsfoot), *Brassica campestris* (summer rape), *B. oleracea* (cabbage), *B. rapa* (turnip), and *Aquilegia vulgaris* (garden columbine). To this list the author adds *Triticum pratense* (red clover). FROST describes the mine as "a large shapeless blotch, with smaller winding galleries conducting to it."

Scaptomyza graminum almost never (in the author's experience) comes to the fermenting fruit bait used to attract Drosophila. Specimens were usually collected by sweeping, and removing the flies from the net with a glass vial. It was found both in the east and in Missouri that *graminum* was collected in deep woods in relatively small numbers. It is more common in lightly wooded regions, especially in the vicinity of oak and maple seedlings, or in some instances in open fields. Probably the best collecting has been in or near patches of red or white clover. Although many clover leaves have been examined for mines, in only one case was a mine found (in red clover) which was certainly made by a *graminum* larva. In this case a pupa was found at the edge of the mine, and the imagine which emerged was identified. Since the adult flies are very abundant in clover patches, especially early in the summer, and since so few mines have been found, it seems probable that the fly is breeding on some other plant which may be associated with the clover.

As STURTEVANT (1921) has pointed out, the genus Scaptomyza is apparently in a transitional stage, in which its members are able to breed either as leaf-miners or as scavengers. HOWARD and MARLATT (1896) report finding it in decaying and fermenting fruit, and MALLOCH and MCATEE (1924) report having bred it from butternut hulls. STURTEVANT has bred it on potato tubers, tomato, and banana.

The author has often found numbers of adults of both *S. graminum* and *S. adusta* around piles of rotting green grass which have stood for two or three weeks. In such piles of grass pupa cases have been found which are apparently those of *S. graminum*.

SEASONAL DISTRIBUTION

In the seasonal distribution a striking difference was noted between New York State and Missouri. In New York the adults first appear in early June

and are fairly abundant throughout the summer and early fall. However, in Missouri adults appear in early May and are abundant in May and June, but become extremely rare, except for a few moist localities, throughout the rest of the summer. This is probably associated with the drying out of the vegetation typifying much of Missouri in late summer. MALLOCH and MCATEE (1924) report *S. graminum* very abundant in the District of Columbia region, and state that it was collected there every month but January.

It seems quite certain that this species is not "winter-killed" as are some Drosophila which survive in the north only if they happen to be situated near human habitations. Unlike the "domestic" species such as *Drosophila hydei* and *Drosophila melanogaster*, which in the north are found only in the vicinity of dwellings in early spring, and later spread out over the countryside, *S. graminum* is as abundant in the early spring in localities remote from human habitation as it is near towns and cities.

CYTOLOGY

The metaphase chromosomes have been described by METZ (1916a, 1916b) who found that in the female there are four pairs: one pair rod-shaped, two

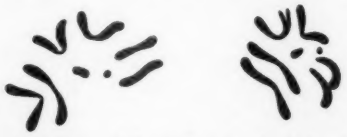

FIGURE 1.—Oogonial metaphase figures of *Scaptomyza graminum* showing the two kinds of microchromosomes. (Acetic-orcein smears from Rochester Strain 7.)

pairs V-shaped, and one pair dot-shaped (the microchromosomes). In the male the rod-shaped chromosomes are unequal in length, indicating that they are the sex chromosomes. Acetic-orcein smears made by the author for the most part corroborated METZ's findings. However, in several New York strains the microchromosomes were short rods, rather than dots, as shown in figure 1. No morphological or physiological characteristics were found to be associated with the presence of these rod-shaped microchromosomes. Larvae and adults were examined which had all possible combinations: two dots, one dot and one rod, and two rods.

Acetic-orcein and carmine preparations of the salivary gland chromosomes showed them to be unsatisfactory for cytological work, since they were extremely small (compared to those of Drosophila) and stained very poorly.

CULTURE METHODS

Scaptomyza graminum is not an easy fly to culture in the laboratory, at least in comparison with many species of Drosophila. It has a relatively long life-cycle and this makes stock cultures particularly liable to various infections and results in drying out of the food cake. The adults have the habit of going down between the food-cake and the side of the bottle and getting stuck there.

The use of regular cornmeal-molasses-agar Drosophila culture medium for

stocks is not too satisfactory. One trouble seems to be that the young larvae are unable to dig into the food. Sprinkling raw oatmeal on the surface of the food, as suggested by DR. W. P. SPENCER, helps somewhat, and DR. J. T. PATTERSON (written communication) has found that using a mixture of agar and Chondrus as a jelling agent makes a softer food into which the larvae can dig. The chief difficulty which the author encountered in raising the species was keeping the cultures free from bacterial infections. Certain types of bacteria grow on the culture medium and produce a transparent, jelly-like mass which overgrows the eggs and larvae and causes the adults to get stuck. Neither increasing the sugar concentrations of the food to high levels nor lowering the pH by means of a phosphate buffer served to keep the cultures permanently free from these bacteria. As might be expected, the bacteria were equally successful on banana agar, plum agar, grape agar, and plain banana food. Although most wild flies collected in New York were free from the bacteria, nearly all Missouri flies were carriers, so that stocks became infected immediately. If the majority of wild flies are carriers, it is patent that the bacteria must be fairly abundant in the natural environment, but that they do not grow sufficiently rapidly in the leaf mines to cause the larvae much trouble. When the fly feeds on or breeds in fruit, bacterial infection would be expected to occur, as it does in the laboratory, which would result in the death of the larvae or eggs. Thus the abundance of this bacteria in Missouri would probably provide a fairly effective barrier to prevent the species from breeding on fruit in that state. Many Drosophila species habitually breed on decaying fruit and so would be expected to be more capable of cleaning up any bacterial infections which might occur. With this point in mind, an attempt was made to keep the stocks in association with larvae of some Drosophila species. Of the species tried (*D. melanogaster*, *D. funebris*, and *D. robusta*) none worked satisfactorily. Even though a small number of Drosophila larvae could clean up the infection in the Scaptomyza culture bottle, they apparently changed the food in some way, since most of the Scaptomyza larvae died, and those which survived pupated while still very small. This was not simply a crowding effect, since as few as five *D. robusta* or 15 *D. melanogaster* larvae in the halfpint culture bottle would result in an extremely low *S. graminum* yield. This difficulty in keeping stocks free from infection was the principal reason the work was finally discontinued.

Experimental cultures were made up in shell vials, using standard Drosophila culture medium seeded with a drop of living yeast suspension. The parent flies were introduced and changed to a fresh vial every two days until fertilized eggs were produced, and thereafter more frequently, depending on the number of eggs laid. When larvae appeared, a half-sheet of Kleenex soaked in yeast suspension was placed in the vial, and the larvae soon crawled into the Kleenex and grew there, finally pupating at the top of the sheet. This method was advantageous since the bacteria grew relatively slowly on the live yeast suspension, allowing the larvae to develop to maturity. One drawback of the method was that the adult flies had to be removed from the vial within two days of the time they emerged or they starved to death. The above rearing

technique is a modification of one introduced by Dr. W. P. Spencer for use with Drosophila.

GENETICS

A total of 1030 wild flies were collected and examined—317 from the Rochester, N. Y., area and 713 from the St. Louis, Mo., area. Thirty-nine New York and 113 Missouri females produced large numbers of progeny in the F1 and F2 and were considered to be "adequately" tested. The New York wild females were tested by allowing them to produce an F1 and then making up eight pair-matings of F1 individuals to produce the F2. Those females in which five or more of the eight pair-matings were successful were considered to be "adequately" tested. The average number of progeny examined per pair-mating was about 50.

In the case of the Missouri wild females, five to eight pairs of F1 flies were mated together to produce a mass F2. In those cases where 125 or more F2 individuals were examined, the female was considered to be "adequately" tested. In both the New York and Missouri material the average number of F1 individuals examined was about 100.

In the later portions of this paper, when the frequencies of mutant genes per wild female are given, these frequencies are calculated entirely from the "adequately" tested females.

Of the abnormalities discovered in the progeny of the wild females, only those are listed here which have been carried as stocks for one or more generations, or have, by their behavior in crosses, shown themselves to be true mutations and not merely developmental abnormalities.

Since the stocks have all been discarded or lost, no genetic symbols have been assigned, since the use of symbols in such cases serves no useful purpose and might cause confusion if any later worker studies the same species. In cases where a name (for example, crossveinless) is used more than once, this does not imply allelism unless such allelism is specifically indicated. When several phenotypically identical mutations were discovered in one locality they are listed under one name except where tests have shown them to be non-allelic. Unless a statement is made to the contrary, all mutants listed showed complete penetrance, good separability, fertility, and viability.

TABLE 1

Summary of Mutant Types Described.

NAME	PHENOTYPIC EFFECT	PENETRANCE	FROM WILD STRAINS
Sex-linked Recessives			
forked-1	Bristles	complete	Rochester 72
forked-2	Bristles	complete	St. Louis 110
cut	Wing shape	complete	Forest Lawn 31
Autosomal Semi-Dominants			
Chutney	Eye-color	complete	Forest Lawn 35
Xasta	Wing-shape	incomplete	Forest Lawn 29

TABLE 1 (*continued*)

NAME	PHENOTYPIC EFFECT	PENETRANCE	FROM WILD STRAINS
Autosomal Recessives			
cardinal	Eye-color	complete	Rochester 65 and 78
plum	Eye-color	complete	Forest Lawn 42 and 28
port	Eye-color	incomplete	Illinois 102
prune	Eye-color	complete	7 Missouri strains
ruby	Eye-color	incomplete	Laboratory stock
peach	Eye-color, bristles	complete	Rochester 1
scarlet	Eye-color	complete	9 Missouri strains
sepia	Eye-color	complete	43 Missouri strains
echinoid	Eye-texture, bristles	complete	Rochester 5
rough-1	Eye-texture	incomplete	Rochester 7
rough-2	Eye-texture	incomplete	Forest Lawn 28
lozenge	Eye-texture, shape	complete	St. Louis 128
margined	Wing-hairs	complete	Forest Lawn 26
plexus	Venation	complete	Forest Lawn 18
net-1	Venation	incomplete	Forest Lawn 32
net-2	Venation	incomplete	Laboratory Stock
curved	Wing-shape	incomplete	Forest Lawn 26
short fifth-1	Venation	complete	Forest Lawn 28 and 31
short fifth-2	Venation	incomplete	Rochester 5
short fifth-3	Venation	incomplete	Forest Lawn 12 and 69
short fifth-4	Venation	incomplete	4 Missouri strains
constricted	Venation	complete	Laboratory stock
miniature	Wing-size	complete	Laboratory stock
crossveinless-1	Venation	incomplete	4 Rochester strains
crossveinless-2	Venation	incomplete	11 Forest Lawn strains
crossveinless-3	Venation	incomplete	3 Missouri strains
round	Wing-shape	incomplete	St. Louis 121
fat	Wing-shape	complete	2 Missouri strains
gnat	Wing-shape	complete	7 Missouri strains
beaded	Wing-shape	incomplete	St. Louis 156
gap-2	Venation	incomplete	St. Louis 148 and 172
stubbly	Bristles	complete	2 Missouri strains
reduced	Bristles	complete	Beck 243
shaven	Bristles and hairs	complete	Forest Lawn 18
duplex	Bristles	incomplete	Laboratory stock
missing	Bristles	complete	Fenton 250
forked-scute	Bristles	complete	Forest Lawn 62
javelin-1	Bristles	incomplete	Rochester 6
javelin-2	Bristles	complete	Forest Lawn 12 and 30
javelin-3	Bristles	incomplete	9 Missouri strains
spineless	Bristles	complete	St. Louis 119
tiny bristles-1	Bristles	complete	Forest Lawn 35
tiny bristles-2	Bristles	complete	Mendon Ponds 98
minute-like	Bristles	complete	Forest Lawn 48
stubbloid-1	Bristles	complete	Laboratory stock
stubbloid-2	Bristles	complete	Rochester 26
speck	Thoracic spot	incomplete	St. Louis 126

DESCRIPTION OF MUTANTS

forked-1—Sex-linked recessive. Bristles on head, thorax, and abdomen are strongly forked. Hairs are unaffected. Apparently a parallel of forked or singed in Drosophila. Rochester strain 72.

forked-2—Sex-linked recessive. Phenotypically similar to forked-1, but lost before it could be tested for allelism. St. Louis strain 110.

cut—Sex-linked recessive. Wings narrowed and scalloped at the tip. Eyes, bristles, and abdomen normal. This may be a parallel of the sex-linked cut-notch in *Drosophila melanogaster*. Forest Lawn, N. Y., strain 31.

cardinal—Autosomal recessive. Bright red eye-color, darkens rapidly, becoming phenotypically wild type in ten to 12-day-old flies. Ocelli not affected. Found in two Rochester strains: 65 and 78.

plum—Autosomal recessive. Dark, translucent eye color. In double recessive cardinal-plum flies the eyes are translucent yellowish-orange in young flies, becoming typical plum color as the flies age. Found in two Forest Lawn, N. Y., strains: 28 and 42.

port—Autosomal recessive. Translucent eye color, slightly lighter than wild type with less prominent shadow. Difficult to separate from wild type apparently because of normal overlaps. Arose in laboratory stock originally from Illinois.

prune—Autosomal recessive. Eyes dark and slightly translucent. Found in seven Missouri strains: St. Louis, Rankin, House Springs, and Wentzville.

ruby—Autosomal recessive. Eye color a little darker than wild type, with very little eye shadow. Difficult to classify and overlaps wild type somewhat. Apparently arose spontaneously from a laboratory stock originally from Forest Lawn, N. Y.

peach—Autosomal recessive. Eye color translucent pink. Bristles reduced to one-half normal length and thickness, wing veins thinner. Peach flies of both sexes show poor viability, males sterile. Rochester strain 1.

scarlet—Autosomal recessive. Bright eye color, lighter than cardinal. Ocelli colorless. Eyes darken slightly with age, but never reach normal phenotype. Homozygous recessive scarlet-prune flies have light orange eyes. Not an allele of cardinal. Found in nine Missouri strains: St. Louis, Rankin, Beck, Fenton, and Wentzville.

sepia—Autosomal recessive. Phenotypically similar to sepia in *Drosophila melanogaster*. Found in 43 strains in Missouri: St. Louis, Desperes, Rankin, Rockwood Park, Beck, Fenton, House Springs, Wentzville, and St. Charles.

echinoid—Autosomal recessive. Eyes rough, bristles about two-thirds normal length and thickness. Echinoid males and females sterile. Rochester strain 5.

rough-1—Autosomal recessive. Eyes slightly roughened, separation from wild type difficult, considerable normal overlaps. Rochester strain 7.

rough-2—Autosomal recessive. Phenotypically similar to rough-1 but less extreme. Forest Lawn, N. Y., strain 28.

lozenge—Autosomal recessive. Eyes narrow, rough and brighter red. Females almost completely sterile. St. Louis strain 128.

Chutney—Autosomal semi-dominant. In homozygous Chutney flies the eyes are dark, opaque brown, becoming almost black as the flies age. In heterozygous Chutney flies the eyes are lighter colored, and there is some difficulty in separating them from wild type. Forest Lawn, N. Y., strain 35.

margined—Autosomal recessive. The long thin hairs on the posterior margin of the wing are missing or displaced. Forest Lawn, N. Y., strain 26.

plexus—Autosomal recessive. Wings show network of extra veins, bases normal. Forest Lawn, N. Y., strain 18.

net-1—Autosomal recessive. Wings show slight network of extra veins, mostly between the distal ends of L3 and L4. Shows normal overlaps in about 60 per cent of the cases. Forest Lawn, N. Y., strain 32.

net-2—Autosomal recessive. Phenotypically similar to net-1. Arose in laboratory stock originally from Mendon Ponds, N. Y.

curved—Autosomal recessive. Wings curved downwards at the tips. Viability poor. Great variability and almost 50 per cent normal overlaps. Forest Lawn, N. Y., strain 26.

short fifth-1—Autosomal recessive. L_5 does not reach the wing margin, usually extends about half-way between the posterior cross-vein and the margin. Found in two Forest Lawn, N. Y., strains: 28 and 31.

short fifth-2—Autosomal recessive. Phenotypically similar to short fifth-1 except that it is much less extreme and gives many normal overlaps. Rochester strain 5.

short fifth-3—Autosomal recessive, phenotypically similar to short fifth-2 except that it is even weaker, giving approximately 60 per cent normal overlaps. Found in two Forest Lawn, N. Y., strains: 12 and 69.

short fifth-4—Autosomal recessive. Phenotypically similar to short fifth-3. Found in four Missouri strains from St. Louis, Rankin, Beck, and House Springs.

constricted—Autosomal recessive. L_3 and L_4 are strongly approximated, wings slightly narrowed distally. Arose in laboratory stock orignally from Forest Lawn, N. Y.

miniature—Autosomal recessive. Wings about two-thirds normal length, not deformed. Wing cells smaller as in miniature of *Drosophila melanogaster*. Both sexes show low fertility. Arose in laboratory stock originally from Rochester, N. Y.

crossveinless-1—Autosomal recessive. Posterior crossveins missing or broken in the middle. Weak and variable in expression, overlaps wild type. Found in four strains from Rochester, N. Y.

crossveinless-2—Autosomal recessive. Phenotypically similar to crossveinless-1. Found in eleven strains from Forest Lawn, N. Y.

crossveinless-3—Autosomal recessive. Phenotypically similar to crossveinless-1, but considerably weaker in expression. Found in three Missouri strains from Desperes and Wentzville.

round—Autosomal recessive. Wings slightly rounded at tips. Shows occasional normal overlaps. St. Louis strain 121.

Xasta—Autosomal semi-dominant. Homozygous Xasta flies have obliquely truncated wings with the marginal vein concave at the wing-tip but intact; angle between veins L_2 and L_5 widened and intercrossvein distance shortened. The hairs and bristles are normal. Heterozygous Xasta flies are less extreme, the obliquely truncated wings being normal in length, but having a distinctly pointed appearance, due to the loss of part of the blade at the distal posterior edge. The heterozygote overlaps wild. Fertility and viability good in both heterozygotes and homozygotes. Wing character similar to dumpy in *D. melanogaster*. Forest Lawn, N. Y., strain 29.

fat—Autosomal recessive. Wings wider and slightly shorter. Unlike fat in *D. melanogaster* the wing venation and bristles are normal. Difficult to separate from wild type, although apparently penetrance is complete. Found in two Missouri strains from St. Louis and Desperes.

gnat—Autosomal recessive. Costal marginal bristles irregular, wings smaller, narrower and darker. Eyes slightly roughened. Found in seven Missouri strains from St. Louis, Desperes, Rankin and Rockwood Reservation.

beaded—Autosomal recessive. Wings with several small notches in the marginal vein between L_1 and L_2. Overlaps wild somewhat. St. Louis strain 156.

gap-2—Autosomal recessive. L_2 does not reach the margin of the wing. Some wild overlaps. Found in two St. Louis strains: 148 and 172.

stubbly—Autosomal recessive. Bristles shorter and stubbier, not as extreme as stubbloid-1. Found in two Missouri strains from Rockwood Reservation and Beck.

stubbloid-1—Autosomal recessive. The long bristles, particularly the dorsocentrals and scutellars are reduced to about two-thirds their normal length and are blunted at the end. Found in forked stock. Recessive epistatic to forked-1.

stubbloid-2—Autosomal recessive. Allele of stubbloid-1 and phenotypically identical. Rochester, N. Y., strain 26.

reduced—Autosomal recessive. Bristles reduced to about one-half normal length, and proportionally thinner. Beck, Mo., strain 243.

shaven—Autosomal recessive. All macrochaetae on head, thorax, and abdomen reduced to thin, wavy hairs, microchaetae about one-half normal length. Females weak and semi-sterile. Forest Lawn, N. Y., strain 18.

duplex—Autosomal recessive. One or more of the dorsocentral and scutellar bristles doubled, with both bristles growing out of one basal ring. Very variable, 60 per cent normal overlaps. Arose in laboratory stock originally from Forest Lawn, N. Y.

missing—Autosomal recessive. One or more of the dorsocentral or scutellar bristles including the basal ring missing. Fenton, Mo., strain 250.

forked-scute—Autosomal recessive. Posterior scutellar bristles reduced to gnarled stumps, all other bristles normal. Forest Lawn, N. Y., strain 62

javelin-1—Autosomal recessive. One or more of the large bristles straight, with slightly swollen tips, hairs normal. Overlaps wild. Rochester, N. Y., strain 6.

javelin-2—Autosomal recessive. Phenotypically similar to javelin-1 but more extreme, rarely overlaps wild. Found in two Forest Lawn, N. Y., strains: 12 and 30.

javelin-3—Autosomal recessive. Phenotypically similar to javelin-1. Found in nine St. Louis, Mo., strains.

spineless—Autosomal recessive. Bristles reduced to one-third normal length and thickness. St. Louis strain 119.

tiny bristles-1—Autosomal recessive. Bristles reduced to about two-thirds normal length and thickness. Forest Lawn, N. Y., strain 35.

tiny bristles-2—Autosomal recessive. Similar to tiny bristles-1 but less extreme. Arose in laboratory stock originally from Mendon Ponds, N. Y.

minute-like—Autosomal recessive. Bristles reduced to one-half normal length and thickness. Fertility and viability poor. Forest Lawn, N. Y., strain 48.

speck—Autosomal recessive. Dark pigmented spots on thorax lateral to post-alar bristles. The name suggests speck in *Drosophila melanogaster;* however, the spots in *D. melanogaster* are differently located, being at the axil of the wing. Shows about 90 per cent penetrance. St. Louis strain 126.

LINKAGE DATA

As mentioned above, this species has a pair of sex chromosomes, two pairs of major autosomes, and a pair of minor autosomes. It is reasonable to expect that there should be one sex-linked linkage group and two large and one small autosomal groups. Below are listed the genes for which linkage data are available. Those names followed by question marks represent genes which definitely do not belong to Group II and probably belong to Group III, since it is unlikely that out of such a small number of genes, any should lie on the minor autosomes.

Group I (X)	*Group II*	*Group III*
forked-1	stubbloid	Xasta
forked-2	plexus	plum
cut	cardinal	minute-like?
	margined	Chutney?
		scarlet?
		missing?

Preliminary linkage tests were made between some of the genes in Group II, including a three-point cross involving cardinal, stubbloid, and plexus. A female homozygous for these three genes was crossed to a homozygous wild type male. The F1 daughters were backcrossed to triple-recessive cardinal stubbloid plexus males. The results of this last cross are summarized in table 2.

From the data in table 2 the following cross-over values are obtained: cardinal-plexus 46 per cent, cardinal-stubbloid 46 per cent, stubbloid-plexus 49 per cent. A two-point cross between plexus and margined gave a crossover value of 45 per cent (433 flies counted). From such data it is not safe to draw conclusions regarding gene order. However, since all pairs of genes tested in

TABLE 2

(see text for explanation)

Wild-type	75	cardinal	56
cardinal stubbloid plexus	53	stubbloid plexus	37
cardinal stubbloid	49	cardinal plexus	45
plexus	56	stubbloid	64
		Total:	435

Group II showed nearly 50 per cent crossing over, it is probable that the second autosome of *S. graminum* shows more crossing over than either of the major autosomes of *D. melanogaster*, which have map lengths of 108 and 106 units respectively.

DISCUSSION

A glance at table 1 will show that of the 52 mutants described, only 31 show complete penetrance. In this respect *S. graminum* resembles *Drosophila funebris*, in which a large percentage of the known mutants are incompletely penetrant. However, the two species differ in that *S. graminum* has a large percentage of eye-color mutations, while in *D. funebris* color mutations of any kind are very rare (SPENCER 1932). Since the mutants detected and studied in *S. graminum* were obviously those giving the clearest expression, the list given above tends, if anything, to exaggerate the percentage frequency of the "good" mutations.

The number of recessive visible mutant genes carried in the heterozygous condition by *S. graminum* wild flies is very high. In the progeny of the 39 adequately tested New York wild females, 37 visible mutant genes were found, while 91 were found in the progeny of the 113 adequately tested Missouri females. The combined data give an average of .84 mutant genes per female tested. The two sets of data are not comparable for a number of reasons. First, the New York F_2 progeny came from the pair matings of F_1 flies, while the Missouri F_2 progeny came from mass matings, and the pair-mating method would be expected to reveal a higher percentage of the mutant genes actually present in the population. Moreover, it is quite probable that some of the mutant F_2 progeny were not recognized in the New York flies due to lack of familiarity with the then new material. The frequencies of mutant genes listed from both New York and Missouri are undoubtedly lowered by the accidental loss of some abnormal flies before they could be adequately tested and the abnormalities shown to be inherited.

A comparison of the above frequencies with those found in Drosophila is difficult because the Drosophila data have been collected and recorded in so many different ways. However, roughly speaking, the percentage of *S. graminum* mutants present in wild populations is a little higher than that found in most Drosophila populations.

Four of the genes described are of special interest because of the number of times they were recovered from wild flies. They are: sepia, scarlet, prune, and gnat. Out of the 113 Missouri females, seven showed prune in the progeny,

nine showed scarlet, 43 showed sepia, and seven showed gnat (see table 3). In the case of the three eye-colors, representative strains from each region were crossed to the St. Louis strains to test for allelism. In every case allelism was indicated. Different strains of gnat were not tested for allelism, since this mutant gene produces a phenotype which is strikingly different from wild type in so many ways that it seems highly improbable that the gnat phenotype would be found several times in the same region and yet depend on non-allelic genes.

The total number of New York females thoroughly tested (39) is rather small; however, it is of interest to note that none of the four genes mentioned above was found in the progeny of any New York flies.

TABLE 3

Frequency of females carrying four commonest mutant genes in Missouri population.

COLLECTING STATIONS*	SEPIA	SCARLET	PRUNE	GNAT
St. Louis (Forest Pk.)	15/46	5/46	3/46	4/46
Desperes	5/7	0/7	0/7	1/7 (18)
Rankin	4/12	1/12	1/12	1/12
Rockwood	3/13 (28)	0/13 (28)	0/13	1/13
Fenton	1/3	1/3	0/3	0/3
House Springs	6/7	0/7	2/7	0/7
South Wentzville	1/5	1/5	0/5 (27)	0/5
East Wentzville	2/5	0/5	1/5	0/5
St. Charles	2/6	0/6	0/6	0/6
Beck	4/9	1/9	0/9	0/9
Totals:	43/113	9/113	7/113	7/113
Percentage Frequencies:	38%	8%	6%	6%

* In each column the figures for the two most widely separated collecting stations are joined by a vertical line. The figure in parentheses in this line indicates the distance in miles between the two stations.

The four genes appear to be spread throughout the St. Louis region. Sepia was found in every locality from which females were tested, scarlet in five out of nine localities, and gnat and prune in four out of nine. Since the numbers of females tested from most stations were extremely small, the fact that scarlet, prune, and gnat did not appear in all collections is not good evidence that their distribution is actually discontinuous. In fact, in spite of the small numbers, the frequencies with which the four genes occurred in the various samples were what would be expected if they were spread throughout the whole St. Louis region.

No flies homozygous for gnat or prune were found in collections. In the case of sepia it is probable that some homozygotes were collected; however, since the eye-color of wild flies varies so much with their age and the environment under which they were raised, classification for sepia in wild flies could not be made with any degree of certainty. One phenotypically scarlet male was collected from Forest Park, St. Louis, but he died without producing offspring, so

it is not certain that he was genetically scarlet, although this seems probable, because no scarlet mimics were ever found in any wild strains.

The repeated occurrence of certain mutant genes in wild flies is well known in several species of Drosophila. For example, the gene light is found in wild strains of *D. repleta* (STURTEVANT 1915; SPENCER 1940a), net in *D. immigrans* (SPENCER 1940b), bobbed in *D. hydei* (SPENCER 1938, 1944), and polychaeta in *D. melanogaster* (TSCHETVERIKOFF 1928).

The New York State F2 progeny came from 11 females collected in Genesee Valley Park, Rochester, N. Y., and from 28 collected in Forest Lawn, nine miles north of Genesee Valley Park. In only one case (crossveinless) were mutations showing identical phenotypes found in the progeny of females from both stations. In the case of crossveinless, 4/11 of the Rochester females and 11/28 of the Forest Lawn females produced crossveinless progeny of the same phenotype. None of these crossveinless strains was tested for allelism, but since mutations to crossveinless may occur at a number of loci in Drosophila, it is possible that here, too, more than one locus may have been involved.

Short fifth-4, found in the progeny of females from four collecting stations in Missouri was likewise not tested for allelism between different stations. But here again the behavior of Drosophila species makes it risky to assume that only one locus was involved.

Although the numbers are small, it seems clear that a real difference existed between the New York and Missouri populations, in that in New York the sub-populations tested were more distinct genetically than those in Missouri.

If a large part of the Scaptomyza population in a given region were killed-off, and the population subsequently built up from a small surviving nucleus, the newly formed sub-populations, being closely related genetically, would be expected to be genetically homogeneous, at least for a time. The genetic structure of the Missouri sub-populations suggests such a killing-off and rebuilding from a small surviving nucleus, while the structure of the New York State sub-populations does not.

The series of severe droughts that have occurred during the past ten years may well explain this difference in the two regions. For example, 1936 was the driest year in Missouri since 1901, while in New York State, somewhat less severe droughts occurred in 1934, 1939, and 1941.

The results of equally low yearly precipitations in the two states are scarcely comparable. In New York a dry year leaves much of the deciduous vegetation alive, while in Missouri the same type of vegetation may be wiped out over large areas. Since Scaptomyza are primarily leaf-miners, climatic differences in the two states would probably be expressed in the size of the breeding population, and ultimately in the genetic homogeneity of the various sub-populations.

SUMMARY

The taxonomy of *Scaptomyza graminum* is reviewed, the imagines are described, and the known distribution given.

The Missouri populations are markedly diminished in size and number

during the late summer, while the New York State populations show much less diminution.

The microchromosomes in metaphase figures may be rod- or dot-shaped. The salivary gland chromosomes are not favorable cytological material.

Culturing *S. graminum* is frequently made difficult by bacterial infections which drown the eggs, larvae, and adults. Such bacteria, occurring in nature in Missouri, may act as a barrier which prevents wild flies from breeding on fruit in that state.

Fifty-two new mutations are described. Of these, three are sex-linked recessives, two are autosomal semi-dominants, and 47 autosomal recessives. Of the 52, only 31 show complete penetrance. In this respect *S. graminum* resembles *Drosophila funebris*.

The frequency of hidden recessives in wild *S. graminum* is somewhat higher than that in wild Drosophila.

Three linkage groups are described. In Scaptomyza, as in Drosophila, there is apparently little or no crossing over in the male.

The Missouri sub-populations are apparently more homogeneous genetically than those in New York State. This may be due to climatic differences affecting population structure in the two states.

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A STUDY OF THE FACTORS AFFECTING FERTILITY OF LOZENGE FEMALES OF DROSOPHILA MELANOGASTER[1]*

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THE reproductive structures and the related phenomena of copulation, fertilization, and oviposition have been widely studied in *Drosophila melanogaster* and related species. NONIDEZ (1920) described the morphology and histology of the various reproductive structures of *D. melanogaster* males and females and traced the course of events in the female between copulation and oviposition. Subsequent studies have been limited to certain structures or to aspects of reproduction.

The normal development of the reproductive structures of *D. melanogaster* has been described by DOBZHANSKY and BRIDGES (1928) and DOBZHANSKY (1930) in their investigations of intersexes. GLEICHAUF (1936) made a detailed study of the male reproductive structures and reported on the variability in shape and structure of various male and female structures. The relationship between the testes and reproductive ducts during development has been reported by STERN (1941) and STERN and HADORN (1939).

Numerous mutants of *Drosophila melanogaster* are known which have abnormal reproductive structures or decreased fertility. HYDE (1914) reported a defect in the female which prevented oviposition. MORGAN (1915) observed that the infertility of "rudimentary" females was due to the retention of eggs. Since that time many other investigators have described anomalies of the ovaries and eggs which were associated with certain mutant genes. Differences in the size and proportions of the reproductive structures in mutant females were reported by DOBZHANSKY (1924, 1927), SCHWAB (1940), and DOBZHANSKY and HOLZ (1943). Two mutant characters affecting the spermathecae have been described by WEXELSON (1928).

One of the manifestations of the mutant gene "lozenge" is infertility, almost sterility, of the homozygous females. Numerous alleles of lozenge have been discovered since BRIDGES in 1916 observed the original lozenge mutant (listed in BRIDGES and BREHME 1944, page 118). Fourteen of these alleles were studied by GOTTSCHEWSKI (1936), who used them in an investigation of qualitative differences between allelic genes. Although his study dealt primarily with the color, shape, and structure of the eyes, some mention was made relative to fertility. OLIVER and GREEN (1944) reported that three of the lozenge alleles showed low fecundity and fertility in homozygous females and that the parovaria and spermathecae were absent in those females. Compounds of those

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alleles also lacked the parovaria and spermathecae, but the females were more vigorous than were the homozygous females.

The existence of abnormalities of the reproductve structures combined with a decreased fertility suggested that valuable information relative to the cause of infertility of the females might be found by studies of the morphology of the ducts, the breeding behavior of the females, and the development of the reproductive structures.

MATERIALS AND METHODS

The lozenge (*lz*) gene is located on the first (X) chromosome at 27.7. Approximately twenty mutant alleles at this locus have been reported (BRIDGES and BREHME 1944), but about half of them have been either lost or discarded. All available lozenge stocks were obtained and used in this study. These included four that were mantained at the UNIVERSITY OF MINNESOTA (*lz^{g}Bx^{2}/ClB*, *lz^{s}/ClB*, *lz^{sB}/ClB*, and *ylz^{v4}/ClB*) and five that were received from the CALIFORNIA INSTITUTE OF TECHNOLOGY (*lz/ClB*, *lz^{3}/f*, *lz^{34k}/ClB*, *lz^{36c}/ClB*, and *lz^{37h}*). In addition, almondex, a lozenge-like gene assigned to the same approximate locus and considered by GOTTSCHEWSKI (1936) as a lozenge allele, was obtained from the CALIFORNIA INSTITUTE OF TECHNOLOGY (*amx/ClB*) and included in the study. Hereafter in this report the homozygous cultures will be referred to respectively as *lz^{g}*, *lz^{s}*, *lz^{sB}*, *lz^{v4}*, *lz*, *lz^{3}*, *lz^{34}*, *lz^{36}*, *lz^{37}*, and *amx*.

Flies were raised in mass cultures at a temperature of 23°±1°C, except where otherwise noted in the section on experiments. The food used was one of the standard corn meal-Karo-agar mixtures, seeded with yeast.

For the study of internal genitalia, etherized females were placed in drops of 0.7 per cent physiological salt solution on a microscope slide. Dissections were made under a 20× dissecting binocular. Sperm teased out of the female receptacles remained motile in the solution in many cases for more than four hours. A cover glass was added, and the fresh material was examined under both low (110×) and high (400×) powers of a compound microscope. Observations were also made under oil. Temporary slides stained with fast green were sometimes used.

Stained serial sections were used exclusively in studying the development of the reproductive ducts. In order to obtain larvae and pupae of desired ages, the life history details recorded by STRASBURGER (1935) were used—that is, larvae that made their way up the sides of the culture bottle and ceased all movements were considered as full-grown; the subsequent eversion of the anterior spiracles was considered to mark the beginning of the prepupal-pupal period. Early pupae were thus selected and isolated in separate vials at two-hour intervals; pupae were then removed and fixed at definite age intervals. In the preparation of pupae older than 12 hours a technique used by BEADLE (reported in D.I.S. 14) was utilized. A thin layer of glue was smeared on a microscope slide, after which the pupae were placed on the surface. After 10–20 minutes the pupal cases were securely fastened to the slide and could be split open by means of a sharp needle. Larvae and pupae were pricked with a fine needle to allow for rapid penetration of fixative. Fixation was made in hot

Bouin's, and the material was allowed to remain in the cooling solution overnight. After two to three hours in the fixative, the anterior one-third to one-half of the specimen was cut off to further facilitate penetration by fixative and succeeding fluids. The material was run through a series of alcohols, alcohol chloroform mixtures, and several changes of chloroform, and was then imbedded in rubber paraffin. Serial sections were cut at 10 microns. The majority of the slides were stained with Delafield's haematoxylin and eosin, but Heidenhain's haematoxylin was also used in some cases.

EXPERIMENTAL RESULTS

Morphology of the reproductive ducts

The internal genitalia of a normal *Drosophila melanogaster* female consist of two ovaries, paired oviducts joining to form an azygous oviduct, a uterus, a single ventral receptacle, two dorsal spermathecae, and two parovaria. These structures are shown in the photomicrographs on Plate 1 (fig. A and B). Structurally, the internal genitalia are as described by NONIDEZ (1920). The oviducts and uterus consist of cuboidal epithelium, lined by a thin cuticle, and surrounded by a layer of muscle. The proximal portion of the uterus, referred to as the vagina, has a thicker cuticular lining, while the distal portion, the uterus proper, has a thin lining and is capable of great distention. The ventral receptacle is a long cuticle-lined tube of cuboidal cells, with a lumen that is very narrow in the proximal end. The two dorsal spermathecae are mushroom-shaped bodies, connected by short narrow ducts to the uterus and lined by thick brown cuticles. The parovaria are large-celled, round to oval "glands" with short narrow ducts emptying into the uterus very close to the openings of the dorsal spermathecae.

OLIVER and GREEN (1944) found homozygous lz^v, lz, and lz^s females to lack the spermathecae and parovaria, although other structures were apparently normal. Females of these three genotypes have been re-examined, together with the other seven homozygous lozenge and almondex stocks and some of the combinations of the various alleles, including non-lozenge. In addition, males of each of the ten mutant genotypes were examined and were found to be normal with respect to their genitalia. In this study, cultures were raised at a temperature of $19° \pm 1°C$.

Thirty females homozygous for each lozenge allele were dissected, except that more homozygous lz^{37} and control (wild type) females were examined because of the variability observed with lz^{37} (see table 1). All the almondex and wild type females had normal internal genitalia. One homozygous lz^{37} female had normal genitalia, but the other 119 lacked at least the parovaria, and 66 of these lacked at least one spermatheca. In females homozygous for any of the other lozenge alleles, no parovaria or spermathecae were observed. In none of the groups were females found in which structures other than the spermathecae and parovaria were noticeably affected.

The appearances of the spermathecae and parovaria in the various females are given in table 1. The table is arranged to show only those parts of the geni-

talia which were present. Those in which the duct and the heavy brown capsule of the spermatheca were present are indicated by the symbol "S," although in many females the capsules were abnormal in shape or size; those having only spermathecal ducts or portions of ducts are indicated by "SD." The parovaria if present are classed as normal, "P," or abnormal, "AP," in

TABLE 1

Portions of the spermathecae and parovaria present in various lozenge females.

GENOTYPE	NO.	oo	1–2 SD	1SD +AP	1S	1S+P OR AP	1S+ 1SD	1S+1SD +P OR AP	2S	2S+AP	2S+P
"+"	100										100
$lz^{37}/+$	30										30
$lz^{34}/+$	30									8	22
$lz/+$	30									9	21
$lz^{9}/+$	30									11	19
$lz^{4}/+$	30									26	4
$lz^{3}/+$	30		1				4		25*		
$lz^{36}/+$	30					3*	1	7	2*	16*	1
$lz^{4B}/+$	30					15		3		3*	9*
$lz^{v4}/+$	30			1		4*	1	6	3*	15*	
$amx/+$	30										30
amx/amx	30										30
lz^{37}/lz^{37}	120	3	17		28*		21*		50*		1
lz^{37}/lz^{9}	30	16	7		5		2				
lz^{37}/lz^{4}	30	28	2								
lz^{37}/amx	20										20
lz^{34}/amx	20									6	14
lz/amx	20									7	13
lz^{9}/amx	20									6	14
lz^{4}/amx	20									18	2
lz^{3}/amx	20		5		2*		7*		6*		
lz^{36}/amx	20							3*		15*	2
lz^{4B}/amx	20					3		1	1	12*	3*
lz^{v4}/amx	20					2*			2*	15*	1
Others**											

* Many of the spermathecae included in this group were incompletely developed or abnormal in shape.

** The thirty females of each of the following genotypes were 100 per cent of the "oo" type: homozygous lz^{34}, lz, lz^{9}, lz^{4}, lz^{3}, lz^{36}, lz^{4B}, lz^{v4}, and the compounds lz^{34}/lz^{37}, lz/lz^{37}, lz^{36}/lz^{37}, lz^{4B}/lz^{37}, lz^{3}/lz^{37}, lz^{v4}/lz^{37}, and lz^{9}/lz^{4}.

"+" refers to wild type or wild type allele.

The symbols used to represent the genitalia are as follows: oo, complete absence of parovaria and spermathecae; SD, presence only of spermathecal ducts; S, presence of capsular portion and duct of spermatheca; P, presence of complete parovaria; AP, presence of abnormal parovaria.

which case only small or rudimentary glands or ducts were present. The symbol "oo" indicates the complete absence of spermathecae and parovaria.

The data in table 1 show that each of the mutant lozenge alleles, with the exception of lz^{37} and *amx*, when heterozygous with the normal allele (lz^{+}) had

some effect on the genitalia, and thus can be considered to be "semi-dominant," at the temperature used, with respect to its effects on the internal genitalia of the female. The lz^{37}, which was completely dominated by lz^{+}, differed from the other lozenge alleles in having variable structures in the homozygous condition and thus was the "weakest" member of the allelic series (where "weak" is used merely to signify a slight deviation from normal, and "strong," a marked deviation). In every tested compound between the various alleles the parovaria were absent and the spermathecae were abnormal or absent, only lz^{g}/lz^{37} and lz^{s}/lz^{37} showed the presence of ducts or spermathecae.

The almondex gene apparently has no visible effect on the female genitalia. Homozygous *amx* females were normal, and all lozenge/*amx* compounds were phenotypically no more extreme than the lozenge/lz^{+} females.

Dissections of the different lozenge genotypes revealed a great variability of the genital structures, even among females of the same genotype as shown in table 1. Perhaps the most striking feature was the wide range in spermatheca structure, varying from complete absence through rudimentary ducts, normal-sized ducts, rudimentary chitinous capsules, irregularly shaped capsules, up to normal and infrequently even accessory spermathecae. It is significant to note that the lozenge genes not only prevented the formation of certain structures, but in some lozenge/lz^{+} females so influenced development that "twin" spermathecae or accessory spermathecae were formed. The parovaria varied from complete absence up through rudimentary ducts, small club-shaped glands, long ducts, irregularly shaped glands, to normal parovaria. Representatives of various genitalia abnormalities are shown in Plate 1 (fig. C, D, E, F).

In the course of making dissections it was found that the phenotype of heterozygous lozenge females (lozenge/lz^{+}) could be modified considerably by varying the temperature at which the flies were raised. In order to measure this temperature effect quantitatively, the following procedure was carried out. Males of lz^{36} genotype were mated to wild type females. The females were allowed to lay eggs in culture bottles over 24-hour intervals, after which the bottles were placed in constant temperature chambers. One group was raised at 19°C; another, at 23°C. (At each temperature, the fluctuation was $\pm 1°$.) Two other groups were raised at 19° up to the pupal and mid-pupal stages and were then transferred to 23°, and vice versa for two other groups. In each group the spermathecae of 25 females were examined. Of those raised at the higher temperature, 24 had normal and one had abnormally shaped spermathecae; of those raised at the lower temperature, eight had normal, five had abnormally shaped spermathecae, and 12 had only one spermathecal capsule. In the groups raised at two different temperatures, only nine of those kept at 19° to the middle of the pupal period developed normal spermathecae, while 24 of those kept at 23° to the middle of the pupal period were normal. Of those kept at 19° to the beginning of the pupal period, 14 were normal; of those kept at 23°, 16 were normal. Although the data are meager, they do suggest that the lz^{36} gene has its major effect on its normal allele at the low temperature. It will be recalled that all the results in table 1 were obtained with flies that were raised at 19°$\pm$1°C.

Sperm motility and genitalia abnormalities

Abnormalities of spermathecae and parovaria in lozenge females suggested that their low fertility might be related to the sperm content in the female. OLIVER and GREEN (1944) found that homozygous lz^g females produced many eggs over an extended period of time, but that fertile eggs were few in number and appeared only during the first few days following copulation. They suggested that the phenomenon might be due to a possible loss of sperm viability in the ventral receptacles of the females.

In order to check on any irregularities in sperm transfer, observations of the sperm were made from the time of copulation to their storage in the tubular receptacle. Fifty-six virgin homozygous lz^g females and 27 virgin wild type females were aged 24 hours, and then each female was placed in an individual vial with five wild type males. Within three hours, 50 of the lozenge and 21 of the wild type females had copulated. In each case, the duration of copulation was carefully timed. This copulation period proved to be significantly shorter in the case of the lozenge females, being 15.1 ± 0.4 minutes as compared to 20.0 ± 0.8 minutes in the wild type females (p is less than 0.0001). Of the 50 lozenge females which did copulate, 14 failed to show any sperm upon being dissected; three of the wild type females which copulated also lacked sperm. This difference in frequency of insemination was not significant, p being equal to 0.19. In those females in which sperm were observed, the sperm could be observed moving in the uterus and in the other parts of the genitalia that were present. Sperm could be seen passing into and up the tubular receptacle.

Matings were then made to determine whether the sperm supply in the receptacles of the females was being depleted rapidly, or whether the sperm were becoming non-motile. Virgin females of the types used by OLIVER and GREEN (1944)—that is, lz^+, lz^g, lz^s, and lz^g/lz^s—were aged 48 hours and then mated to five wild type males in individual vials for 24 hours. At the end of definite time intervals in days, some of the females were dissected and the tubular receptacles examined for sperm content and sperm motility. Visual estimates were made of the number of sperm in the receptacles. Only a rough relative estimate was feasible, and this estimate concerned itself with the quantity of sperm in the ventral receptacle. An arbitrary scale from 0 to 100, with intervals of 10, was set up, with 0 denoting no sperm, and 100, a completely filled receptacle. Although this did not allow for a careful quantitative measurement, it became quite easy to grade the relative content to the closest 10 per cent. The results from these matings and dissections are shown in table 2.

The data in table 2 indicate that the initial amount of sperm stored in the tubular receptacles of lozenge females was less than in those of the control females. However, the most striking feature was the loss of sperm motility in a relatively short time in the lozenge females. Motile sperm were found in only two of the lz^g females that were examined after the fifth day. These two were found on the ninth day after copulation, but in both cases the motile sperm were in the distal end of the receptacle, whereas the proximal end was filled

with a mass of non-motile sperm. These females are "exceptional," insofar as motile sperm were not found in the receptacles of more than 100 other lozenge females (in this and other studies) that were dissected seven days or more after mating. In some females, the non-motile sperm appeared quite normal, except that no movement could be observed. In others, the sperm were twisted into a "rope," often "kinky," which sometimes occupied only the central part of the lumen proximally. Normal sperm and a "rope" of non-motile sperm from

TABLE 2

Sperm content and motility of sperm in tubular receptacles of females.

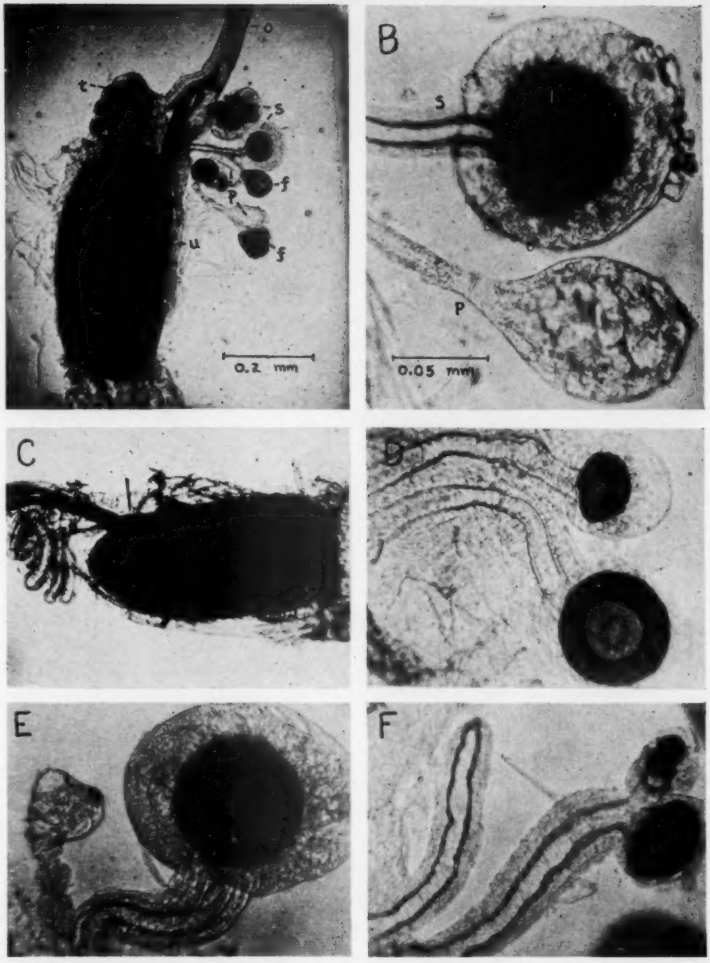
GENOTYPE	DAYS AFTER COPULATION	1*	5	7	9	11
lz^+	Total examined on each day	30	29	14	20	13
	Number having sperm	26	27	13	20	11
	Number having motile sperm	26	27	12	20	11
	Average sperm content**	98	82	68	57	42
lz^g	Total examined on each day	40	30	13	19	9
	Number having sperm	28	20	8	14	6
	Number having motile sperm	28	4	0	2	0
	Average sperm content	75	44	39	29	33
lz^s	Total examined on each day	30	29		15	
	Number having sperm	6	16		5	
	Number having motile sperm	6	4		0	
	Average sperm content	78	35		24	
lz^g/lz^s	Total examined on each day	30	31		20	
	Number having sperm	22	22		9	
	Number having motile sperm	22	2		0	
	Average sperm content	76	25		13	

* The first day represents the 24-hour mating period.

** The average sperm content is given in percentage, based upon visual estimates of the quantity of sperm in the tubular receptacle, with 0 denoting no sperm and 100 denoting a receptacle filled with sperm. The average sperm content is based only on females containing sperm.

a lozenge female are shown on Plate 2 (fig. A, B). The loss of sperm motility was observed in females of all three lozenge genotypes but not in the controls.

Day-to-day records were kept of the number of offspring produced by the females before they were dissected. The breeding results substantially corroborate the results reported by OLIVER and GREEN (1944) and are therefore not reported here. In general, offspring were produced by control (lz^+) females throughout the test, but most of the progeny of lozenge females appeared during the first three days. However, one offspring was produced by a homozygous lz^g female on the fifth day and one by a homozygous lz^s female on the fifth and also the sixth day. The breeding results parallel the decrease in sperm motility very strikingly.



EXPLANATION OF PLATE 1

All the photomicrographs included on this plate were taken of unstained material. Figures A and C are of the same magnification, and figures B, D, E, and F are of the same magnification.

FIGURE A.—Reproductive tract, exclusive of ovaries, of wild type female. s indicates spermathecae; p, parovaria; o, oviduct; t, tubular receptacle; f, fat bodies; and u, uterus with egg inside.

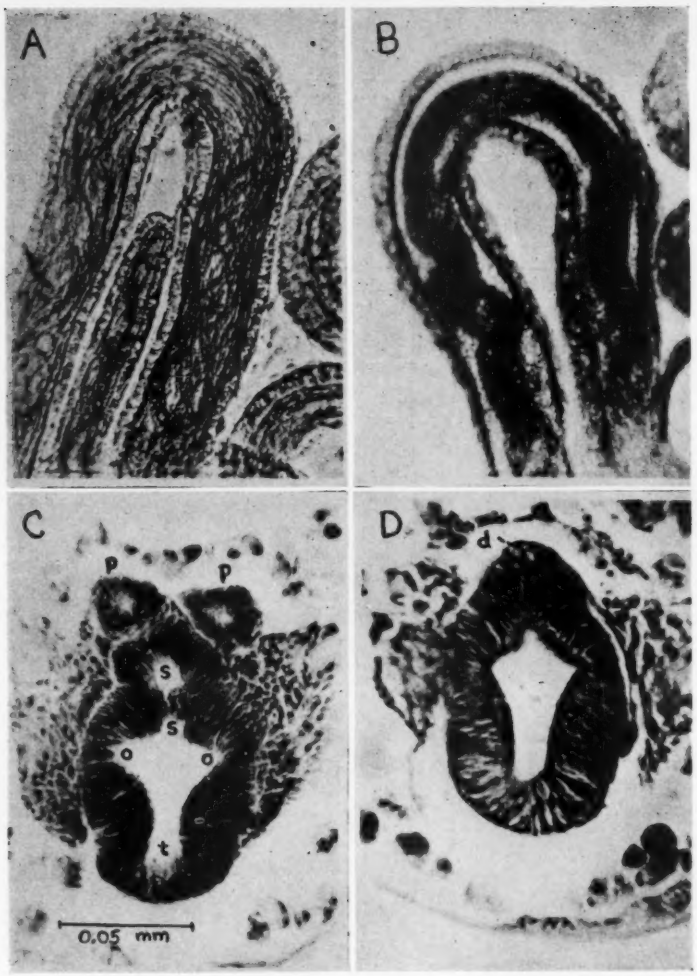
FIGURE B.—Spermatheca and parovarium of wild type female.

FIGURE C.—Reproductive tract of lz^{sB}/lz^{37} female. No parovaria or spermathecae are present.

FIGURE D.—Spermathecae of homozygous lz^{37} female, showing variation in size.

FIGURE E.—Abnormal parovarium and normal spermatheca of $lz^{36}/+$ female.

FIGURE F. "Twin" spermathecae and undeveloped spermatheca (duct only) of $lz^{3}/+$ female.



EXPLANATION OF PLATE 2

All the photomicrographs included on this plate are of the same magnification.

FIGURE A.—Portion of tubular receptacle of wild type female filled with sperm. The sperm were very motile at the time of dissection. Unstained preparation.

FIGURE B.—Portion of tubular receptacle of homozygous *lz*^{g} female nine days after copulation. The sperm were non-motile at the time of dissection, and as shown here, present a fuzzy "rope"-like appearance. Unstained preparation.

FIGURE C.—Transverse section through genital imaginal disc of 18-hour wild type female pupa. Note parovaria (p), spermathecae (s), and beginnings of tubular receptacle (t) and paired oviducts (o). Stained preparation.

FIGURE D.—Transverse section through genital imaginal disc of 18-hour homozygous *lz*^{g} female pupa. Compare with preceding figure, noting absence of parovaria and spermathecae. The dorsal layer of the disc shows some signs of differentiation (d). Stained preparation.

Relationship between degree of spermatheca abnormality and fertility

Although the internal genitalia are abnormal in many homozygous lz^{37} and lz^{37}/lz^{g} females, these females are often fertile. This fact suggested that some relationship might exist between fertility and structure of internal genitalia. As a test of this possibility, virgin lz^{37} and lz^{37}/lz^{g} females were aged 24 hours, kept with males for 24 hours, transferred daily into fresh vials for nine days, and then dissected. Counts were made of the offspring production for each day. Only females which contained sperm or produced offspring are included in the following data. In the lz^{37} group, one female which lacked both parovaria and spermathecae produced 165 offspring; ten females which lacked parovaria but had either one or two spermathecal ducts produced an average of 9.1 ± 8.4 offspring; and 71 females lacking parovaria but having one or two spremathecal ducts and capsules produced an average of 212.7 ± 10.5 offspring. The figures for the corresponding three groups of lz^{37}/lz^{g} were: 40 females with an average of 1.9 ± 1.1 offspring, 14 females with an average of 4.5 ± 2.3 offspring, and 21 females producing an average of 228.1 ± 21.6 offspring. A control group of 24 wild type females, with normal genitalia, produced an average of 451.1 ± 24.0 offspring.

In both lozenge genotypes those females in which spermathecae (capsules) were present showed a much higher fertility than did those lacking spermathecae or possessing ducts only. However, the average offspring production figures for all lozenge groups were significantly less than that for the control females. One lz^{37} female belonging to the group with spermathecae (capsules) produced 457 offspring, thus exceeding the mean for control females. The performance of the single lz^{37} female in the first group (lacking capsules and ducts) which produced 165 offspring appears almost to reverse the situation. However, an examination of the day-to-day record of this female showed that the offspring appeared only during the first three days after the mating period. This behavior is similar to that observed in some of the "highly-fertile" homozygous lz^{g} and lz^{s} females, in which upwards of 100 offspring are produced in the two to three days following copulation, although both of these genotypes lack parovaria and spermathecae. One lz^{37}/lz^{g} female which had a spermatheca has not been included in the above data because she apparently presents a special case. She had one spermatheca, but the duct leading to it was closed in the proximal portion. There were no sperm distal to this closure. This female produced no offspring.

The relationship between the type of anomaly of the internal genitalia and the length of the productive period of the females is shown in table 3. Only those females that lived for the nine days of the test are included. Parovaria were absent in all but the control females. The table is arranged so as to show how many of each type of female produced offspring only one day, two days, etc. As an example, 71 lz^{37} females had one or two spermathecal ducts with capsules, many of which were abnormal in shape or size. Of these females, one produced no offspring (although sperm were present in her ducts); two became sterile after two productive days; two more, after the third day; and so on,

with 13 being fertile on the ninth day. All the control females were fertile for from six to nine days. Many of the lz^{37} and lz^{37}/lz^{9} females with capsules and ducts were fertile into the second half of the test period. However, the females lacking spermathecal capsules were either sterile or were fertile only during the first two or three days of the test.

The data show that the presence of spermathecae, the capsular portion specifically, is accompanied by a prolongation of the fertile period following copulation and by increased fertility of the lozenge females. When the females were dissected after the ninth day, sperm in the ducts of the females with

TABLE 3

Relationship between the conditions of the spermathecae and the maximum productive period of females.

GENOTYPE	PHENOTYPE**	NUMBER OF FEMALES REMAINING FERTILE FOR DAYS AFTER MATING									
		NO. WITH SPERM	NO. STERILE	1*	2	3	4	5	6	7	8	9
lz^{37}/lz^{37}	Ducts and capsules (S)	71	1	70	70	68	66	59	41	27	15	13
lz^{37}/lz^{37}	Ducts only	10	4	6	5	2	0	0	0	0	0	0
lz^{37}/lz^{37}	No ducts	1	0	1	1	1	0	0	0	0	0	0
lz^{37}/lz^{9}	Ducts and capsules (S)	21	1	20	20	20	18	16	12	5	1	1
lz^{37}/lz^{9}	Ducts only	14	10	4	4	0	0	0	0	0	0	0
lz^{37}/lz^{9}	No ducts	40	32	8	8	0	0	0	0	0	0	0
"+"	Normal	24	0	24	24	24	24	24	24	23	22	20

* The first day represents the 24-hour mating period.

** All the females except "+" lacked parovaria.

capsules were usually motile, but those in females without capsules were nonmotile in almost all cases.

Fertility of almondex females

Homozygous almondex females have been reported to be sterile. They differ, however, from the (other?) lozenge alleles in that their internal genitalia appear normal (see table 1). Therefore, the factors involved in this sterility and those in the case of lozenge females probably differ. Thirty virgin almondex females were aged 24 hours and mated individually for 24 hours to five wild type males. The females were transferred to fresh vials on the fourth and fifth days and were dissected after the sixth day.

Seven of the 30 almondex females were fertile. They produced 18 offspring, eight of which appeared during the first four days, one on the fifth day, and nine on the sixth day. These offspring consisted of 12 females which emerged, three females which failed to emerge, and three flies which failed to emerge and could not be identified as to sex. Numerous eggs were produced by almost all the females, and 24 of the 30 females had sperm (motile in all cases) in their ventral receptacles on the sixth day after mating. The amount of sperm re-

maining after six days was unusually high, averaging more than 80 per cent of capacity. The infertility of almondex females thus differs strikingly from that of lozenge females in that the very low fertility in almondex is not associated with loss of sperm motility. It appears that the infertility of almondex females may be due to egg defects or zygotic lethals, as indicated by the death of numerous pupae. The one-sided sex ratio (15 females to 0 males) suggests that the male zygotes die early in development. Studies on this problem are being continued.

Comparison of development of internal genitalia of lozenge and wild type females

The internal genitalia of Drosophila have a dual origin. The gonads arise from the early polar cells, but the remaining structures develop from an ectodermal disc and adjacent mesoderm. The ovaries of lozenge females are apparently normal and, therefore, were not studied.

In the study of the development of the reproductive ducts, serial sections were made of homozygous *lz*^{g} and wild type female full-grown larvae and pupae. The pupae were selected at six-hour age intervals, ranging from 0 to 36 hours, and also at 48, 72, and 96 hours. At the temperature used (23° ± 1°C), females of both types emerged at approximately 108 hours.

The development of the female genitalia in *Drosophila melanogaster* has been described briefly by DOBZHANSKY (1930), and in *D. virilis*, more completely by NEWBY (1942). Since the present report has as its primary interest the differences in development of *lz*^{g} as compared to normal wild type females, only those points will in the main be considered.

Up to the time the genital pore is formed, the development of the genital disc in *D. melanogaster* corresponds to that in *D. virilis*. However, the formation of the parovaria and spermathecae takes place somewhat differently from that described by NEWBY for *D. virilis*. In *D. melanogaster* a moderate dorsal evagination of the disc occurs. At about 12–15 hours of pupal life a pair of grooves appear in the posterior portion of the evagination and push out dorso-anteriorly as ducts. During this same pupal period two median ducts form from the anterior portion and push out dorso-anteriorly from the evagination, one ahead of the other. The posterior pair of ducts develop into parovaria, and the anterior pair become spermathecae. In the anterior portion of the lumen of the disc a ventral groove appears by the 18th hour and develops into the ventral receptacle. The anterior cavity proper develops as the oviduct, dividing into two branches at about 20 hours and reaching the ovaries at about 40 hours.

The imaginal disc of the full-grown *lz*^{g} female larva resembles that of the wild type female. Differences between the imaginal discs of *lz*^{g} and wild type females become evident early in pupal development. The beginning of the dorsal evagination appears clearly in the six-hour wild type female pupa, but in the *lz*^{g} pupa of the same age there is little if any dorsal differentiation of the disc. In the 12-hour pupae, the difference becomes more marked. The rudiments of the parovaria are recognizable in the wild type pupa at this time,

but no comparable structures are visible in the lz^g pupa. The developing parovaria and spermathecae become more distinct in the wild type 18-hour pupa; in the corresponding lz^g disc there are signs of a thickening or early differentiation of the dorsal layer (Plate 2, fig. C, D), but this apparent differentiation goes no farther, and no signs remain of it in the 48-hour lz^g pupa. The development of the oviducts and tubular receptacle in the lz^g pupa proceeds as in the wild type female. The development of the abnormal genitalia of lz^g females can thus be attributed to the failure of the dorsal layer of the imaginal disc to differentiate properly during the first 12 hours of pupal life.

DISCUSSION

The lozenge alleles have been studied as a group by only one worker, although they have been used in many diverse experiments. GOTTSCHEWSKI (1936) noted the great variability of the lozenge alleles and found it possible to break them up into three distinct groups on the basis of eye characters: (1) "blood-red" alleles, (2) brown alleles, and (3) almondex. The first group, with many representatives, he characterized as having rough, glossy, blood-red eyes; the second, also with many representatives, as having smooth, "rimmed," brown eyes; and the third group, represented only by almondex, as having small eyes with a brownish "shimmer." GOTTSCHEWSKI reported various degrees of infertility in the different groups. He believed that the infertility of the first two groups was not related, because females heterozygous for genes in the two groups proved to be fertile, although the homozygous females were sterile. GOTTSCHEWSKI also found differences between the first two groups with respect to their effects when in combination with other eye color genes. From his experimental data and from other data in the literature, GOTTSCHEWSKI concluded that qualitative differences in the end action of single phases of polyphenic alleles are due to qualitative differences of such alleles either in their whole nature or at least in some phases, and that consequently members of the same allelic series may behave as genes of different loci with respect to interaction.

Similarity in effects of lozenge alleles

The data in table 1 suggest that the nine lozenge alleles in their action on the internal genitalia of the females present a homogeneous series of genes. All of the alleles caused abnormalities of the reproductive structures. Females homozygous for each of the alleles except lz^{37} lacked any sign of the parovaria or spermathecae. All except one of 120 lz^{37} females lacked parovaria, and although 100 of them did have one or two spermathecae, the capsules in many were abnormal in size and shape. The interactions between lz^{37} and each of the alleles suggest a similarity in basic gene action with respect to the development of the reproductive structures. All but two of the alleles interacted in compound with lz^{37} to cause the absence of the spermathecae and parovaria. Two lz^{37}/lz^{a} females had spermathecal ducts, but 28 had no sign of the parovaria and spermathecae. Fourteen of 30 lz^{37}/lz^{g} females had spermathecal ducts or ducts and capsule. All the alleles except lz^{37} interacted in compound with

lz^+ to produce abnormalities of the genitalia in some of the females, although they differed somewhat in the degree of effect.

The three groups of alleles which GOTTSCHEWSKI formulated according to the action of the genes upon eye-color and eye-structure do not accurately separate them into groups with respect to their action upon the genitalia. Alleles lz^s and lz^{sB} are identical in the external structure and color of the eyes. However, they interact to different degrees with lz^+ (table 1) and to a lesser extent with lz^{37} in the development of the spermathecae. Alleles lz^s and lz^g belong to separate groups as determined by the characteristics of the eyes, yet they react more or less alike with lz^+ and with lz^{37} in the development of the spermathecae. Females homozygous for either lz^s or lz^g are also very infertile (GREEN and OLIVER 1941) and lack parovaria and spermathecae, and the sperm stored in the females lose their motility soon after copulation (table 2). The compound lz^g/lz^s also causes absence of parovaria and spermathecae and loss of sperm motility, but the fertility of the females is increased over either homozygote.

With respect to the almondex gene, the present work bears out GOTTSCHEWSKI's consideration of it as a group separate from the other lozenges. However, whereas he found interaction between one of his "group 1" lozenges (lz^{35}) and almondex with respect to eye characteristics, the present work shows no similarity between any of the lozenges tested and almondex with respect to effects on genitalia and fertility. This would argue against the consideration of almondex as one of the lozenge alleles.

Semi-dominance of lozenge alleles

It is interesting to note that the lozenge alleles give observable effects on the genitalia of females having one lozenge and one normal gene (see table 1), although the eyes of these females are apparently normal. Only one allele, lz^{37}, was completely suppressed by the normal allele. Some of the females heterozygous for either lz^{34}, lz, lz^g, or lz^s had at least abnormal parovaria. The other four alleles had even stronger effects in heterozygous condition. With at least one of the alleles, the degree of effect of the lozenge gene upon the normal allele is dependent upon the temperature to which the flies are subjected. Flies with the genotype lz^{31}/lz^+, for example, generally have normal genitalia if they are raised at 23°C, but many have abnormal genitalia if the development occurs at 19°C. Thus, genes which have been considered previously as typical recessives actually act also as "semi-dominants" in one of their effects. So-called dominance and recessiveness are, of course, not always clear-cut and are greatly modified by genetic and environmental factors.

Causes of infertility of lozenge females

From the data presented on breeding behavior, it appears that the infertility of lozenge females is due to a complex of causes. Most apparent of these is the absence or abnormalities of spermathecae, which might conceivably represent a decrease in sperm-storing capacity. Likewise, the 25 per cent decrease in copulation time as observed in lz^g as compared to lz^+ and the lesser amount of

sperm initially stored in the tubular receptacle of the lozenge females shown for lz^g and lz^s in table 2 indicate some deviation from normal.

The most striking and probably the most important factor involved is the drop in motility of sperm in the ducts of the female. This loss of sperm motility in lz^g, lz^s, lz^g/lz^s and in lz^{37} females lacking capsules accounts very satisfactorily for the very brief period of fertility of lozenge females, a condition which at first seemed quite puzzling. At one time it was thought that egg failure might be responsible for this curtailment of fertility, but by a technique of double matings it was shown that this could not be the case (ANDERSON and OLIVER 1942).

In that study, homozygous lz^g females were mated to wild type males. After the females had lost their fertility, they were mated to males which carried $M\hat{e}/H$ on their third chromosomes. Many of the females which had become "sterile" regained their fertility with the second mating. In the present report, the sperm which are stored in the tubular receptacles of lz^g and lz^s females lose their motility within a few days after copulation (table 2). Sperm may still be found in the tubular receptacle after that time, but they are often clumped together. Only those in the lumen distal to the aperture will show any movement. The lz^g and lz^s females, it will be recalled, produce progeny only during the first two or three days after copulation.

Other factors are also evidently involved in the infertility, for females of similar phenotype with respect to the genitalia, but of different genotype, show significant differences in fertility (OLIVER and GREEN 1944). A number of cases of female sterility and infertility in various mutants have been reported in the literature (for example, CLANCY and BEADLE 1937), but none have involved sperm inviability. However, sperm inviability has been found by several workers to play a part in Drosophila interspecific crosses—namely, by D. D. MILLER (DOBZHANSKY 1941, page 271), and PATTERSON, STONE, and GRIFFIN (1942). In these cases only non-homologous sperm underwent degeneration, whereas in the present case of lozenge females all sperm (from lozenge or wild type males) were affected.

Significance of parovaria and spermathecae

The data on fertility of the lozenge females presented in this paper indicate the significance of various female reproductive structures. The parovaria have been a stumbling block to all would-be interpreters of Drosophila genitalia and are difficult to homologize with any of the structures of other insect groups (HEBERDEY 1931). NONIDEZ (1920) observed the gland-like structure and the refractile granules in its fluid and suggested that the parovarian secretion may activate the sperm or perhaps dissolve the thick portion of the ejaculate, but added that the function is obscure. Since then, workers have added little to these remarks. GOTTSCHEWSKI (1937) attributed his difficulty in artificially inseminating Drosophila females with sperm from the seminal vesicles of the males to the lack of parovarian secretion, although he was suc-

cessful in two cases (only three offspring, however). That both of these functions suggested by NONIDEZ are non-existent is shown in the present work in which females lacking parovaria (for example, lz^g and lz^e) contain active sperm during the first few days following copulation and are fertile during that period. Moreover, lz^{37} and lz^{37}/lz^g females with one or two spermathecae, but with no parovaria, produced approximately half as many offspring as did the wild type females (212.7 and 228.1 as compared to 451.1), and as shown in table 3, the sperm remained motile in the tubular receptacles for more than nine days. This may suggest that the parovaria are important in the control of fertility, but it must be remembered that the spermathecae of many of these females were small or abnormal in shape. Though the absence of parovaria may be a contributing factor, the evidence does not support the significance attributed by NONIDEZ to the parovaria in normal reproduction.

The two dorsal spermathecae have been described as sperm-storing structures (NONIDEZ 1920) which also function as secretory structures, the secretion serving in the maintenance of sperm viability (HEBERDEY 1931). In his phylogenetic study of the reproductive structures of the Insecta, HEBERDEY regarded these two dorsal spermathecae of Drosophila as true seminal receptacles. The data on lz^{37} and lz^{37}/lz^g females bear this out. Those females having no ducts or having ducts but not capsules were with only a few exceptions either sterile or very infertile. They produced fewer than ten offspring on the average and produced no progeny after the third day following copulation (table 3). Females with ducts and capsules retained their fertility for a longer period of time. Some of them remained fertile for the nine days of the test, although the proportion of such fertile females was much less than the proportion of control females which remained fertile for that period of time. As was mentioned, the lz^{37} and lz^{37}/lz^g females were less fertile than the control females. The dorsal spermathecae evidently function in sperm maintenance through the elaboration of some secretion or by some similar means. It is very difficult to ascertain the exact manner in which they function, but it is quite evident that they are necessary for any degree of normal fertility.

HEBERDEY did not believe the ventral tubular receptacle of various Diptera (including Drosophila) to be a primary seminal receptacle, but instead considered it to be simply an outpocketing of the vagina (similar to a *bursa copulatrix*) which in many cases has taken over the functions of a seminal receptacle. The data on lozenge females fit this explanation very well also, for the tubular receptacle in the absence of the dorsal spermathecae and parovaria functions in sperm storage, but fails to maintain the sperm over an extended period of time. In females which lack the capsular part of the spermathecae, the sperm stored in the tubular receptacles clump into a non-motile mass.

Although the present work gives some evidence of the significance of the various female reproductive structures, a complete picture remains yet to be drawn. It will take additional studies on various mutants as well as studies on experimentally altered females before various dubious points can be cleared up. However, the extensive use of Drosophila in genetic and evolutionary

studies calls for a clearer interpretation of the reproductive phenomena both in normal and mutant stocks.

Effect of the lz^g allele on the development of genitalia

The developmental study reported upon in this paper was carried out with the purpose of determining the manner in which the abnormality of lozenge female genitalia arose. The absence of parovaria and dorsal spermathecae in the homozygous lz^g female and probably in females homozygous for the other lozenge alleles is due to irregular development of the genital imaginal disc. This deviation from normal is first apparent in the six-hour pupa, but very likely is present in even earlier stages. In lz^g females, the dorsal cells of the imaginal disc fail to differentiate into genital ducts. A dorsal evagination appears in lz^+ females by the sixth hour of pupal life and continues to develop into the parovaria and spermathecae. Although a feeble and abortive differentiation of the dorsal cells in the genital disc of the lz^g pupa occurs between the twelfth and twenty-fourth hours, all signs of this differentiation disappear by the forty-eighth hour. The dorsal portion of the imaginal disc in lz^g females, therefore, remains undeveloped. The presence of a temperature-sensitive period near the time of pupation as shown in $lz^{36}/+$ may fit in with the developmental picture in that the temperature-sensitive period occurs at about the time of the expected differentiation of the dorsal evagination.

It is of interest to compare the irregularity in lz^g genitalia development with the irregularity in eye development reported by WADDINGTON and PILKINGTON (1943) for one of the lozenge mutants. They found that the abnormal adult eye of lz^s flies resulted from a failure of the cells of the middle layer of the eye to penetrate between the cells of the outer layer in early pupal life, with a later failure of the retinulae to penetrate the basal layer. Although the anomalies of the genitalia seem also to be related to the failure of the cells to differentiate normally, it seems unwise at present to speculate on the relationship between these developmental irregularities in eyes and genitalia.

SUMMARY

Parts of the female genitalia, parovaria and spermathecae, have been found to be absent or abnormal in nine different lozenge alleles of *Drosophila melanogaster*, and in all except lz^{37} the lozenge genes have been found to behave as "semi-dominants." The male genitalia are not affected. The lozenge alleles show interaction effects on the genitalia of the females, with evidence of incomplete dominance between some alleles.

The gene almondex (*amx*) has no effect on the genitalia, and has no modifying effect on females that are heterozygous lozenge/*amx*. Homozygous almondex females are very infertile, and the progeny which occur are all females. The infertility of almondex females does not resemble that of lozenge females.

The genotype lz^{36}/lz^+ is very sensitive to temperature changes, with the sensitive period occurring at about the time of pupation.

The infertility of lz^g females (and probably other lozenges) is apparently due to a number of factors, including a shorter copulatory time, smaller initial

storage of sperm, possibly a smaller sperm-storing capacity, and degeneration of sperm within the tubular receptacles of the females.

The dorsal spermathecae are evidently necessary for high offspring production and extended sperm viability, as demonstrated by differences in fertility and in sperm motility between females with and without dorsal spermathecae but of similar genotype.

Females lacking parovaria but having the capsular portions of the spermathecae are able to produce great numbers of offspring over an extended period of time, indicating only minor or supplementary functions on the part of the parovaria in sperm viability and in fertility of female.

The tubular receptacle is not able to maintain sperm over an extended period of time in the absence of the spermathecae and parovaria.

Abnormal differentiation of the genital imaginal disc in the *lz*^{g} female becomes apparent within the first six hours of pupal life. Cells of the dorsal layer fail to differentiate properly, and the parovaria and spermathecae which normally develop from this layer are absent.

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A GENE IN DROSOPHILA MELANOGASTER THAT TRANSFORMS FEMALES INTO MALES

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A CULTURE, counted in April, 1944, gave 20 males of an unexpected phenotype (wild type for a series of sex-linked alleles) that could not be accounted for by any of the usual interpretations current in Drosophila genetics. These males were sterile, but studies of descendants of their sibs have shown their nature.

It is now clear that these were XX diploids—that is, had the usual composition of normal females, but were homozygous for a third chromosome recessive gene that may be called "transformer" (symbol *tra*). Heterozygotes (*tra*$^+$/*tra*) do not differ from wild type in any way yet detected, nor do XY *tra*/*tra*—that is, the gene is recessive and also has no effect on males. XX *tra*/*tra* individuals appear like normal males. They have fully developed sex-combs, male-colored abdomen, normal male abdominal tergites, anal plates, external genitalia, genital ducts, sperm pump, and paragonia, and show the usual rotation of the genital and anal segments through 360°. They mate with females readily and normally. The testes, however, while normal in color, elongate, curved, and attached to the ducts, are much reduced in size. The testis size is variable, but in no case does it approach that found in the normal brothers. In two respects these specimens resemble females: they are often larger than their XY brothers, and they more often appear in first counts from cultures, suggesting that their development rate approaches that of females.

These XX *tra*/*tra* individuals are all wholly sterile. It seemed possible that this was due to their not carrying a Y chromosome. Since the gene is an autosomal recessive, it was easy to transfer it to an attached-X line, and to obtain $\widehat{XX}$ Y *tra*/*tra* specimens. These differ in no way from those without a Y, and are equally sterile. These same cultures should give $\widehat{XX}$ X *tra*/*tra*—that is, superfemales homozygous for the new gene. In a large series of cultures only one such specimen has been obtained, indicating that the gene does not increase the usual very low viability of superfemales. This one specimen had the beaded wings characteristic of superfemales, but had the male genitalia of XX *tra*/*tra;* it did, however, have sex-combs with only about half the normal number of teeth, and accordingly may be taken as indicating that superfemales are not as strongly modified toward maleness as are ordinary females—perhaps the best support yet produced for the view that superfemales are more "female" than are females.

The gene has also been introduced into a triploid line. 3X3A *tra*/*tra*/*tra* triploids resemble the corresponding diploids—that is, they are males with large wing-cells and ommatidia, with small testes, and they are sterile. Unfortunately, as the experiment was carried out, the 2X3A (triploid intersex) classes could not all be identified with certainty; however, large numbers of

possible 2X3A *tra/tra/tra* were tested, and no fertile males were encountered. It seems certain that such specimens are sterile, and it is probable that they still have the abnormal wings and eyes usual among triploid intersexes. It is not known whether one or two doses of *tra* have any influence on the sex grade of triploid intersexes.

A few preliminary tests having indicated that *tra* lies in chromosome III, it was balanced against "*Dcx*", a third chromosome carrying the dominant Dichaete (lethal when homozygous) and a complex rearrangement that usually prevents effective crossing over except near the ends of the chromosome. A few sample results follow:

♀ w^a/w^a *Dcx/tra* × ♂ w^+ *Dcx/tra* → 108 ♀ *D*, 78 ♂ +, 120 ♂ *D* w^a, 63 ♂ w^a (plus 1 ♂ *D*, due either to non-disjunction of the X's of the mother, or to crossing over between *D* and *tra*).

♀ w^a/w^a *Dcx/tra* × ♂ w^+ *tra/tra* → 64 ♀ *D*, 50 ♂ +, 47 ♂ *D* w^a, 60 ♂ w^a.

♀ $\widehat{yv}$ *Dcx/tra* × ♂ w^a *tra/tra* → 137 ♀ *y v D*, 1 super-♀ + (described in text), 126 ♂ *y v*, 194 ♂ w^a *D*, 190 ♂ w^a (plus 1 ♂ *y v D* evidently due either to detachment of the X's of the mother or to crossing over between *D* and *tra*).

Using this strain it is easy to get males known to be homozygous for *tra*, and accordingly tests for its locus in chromosome III can readily be made. The methods used are not new in principle, so it need only be stated that they show the gene to lie between *st* (locus 44.0) and *cp* (locus 45.3). This places it in the left limb of III (=element D).

The effects of *tra* on the phenotypes of mutant characters showing sexual dimorphism have been studied in a few cases. Scute-3 is lethal in females but fully viable in males (DUBININ 1933). It appears that this lethal effect is not overcome by homozygous *tra*—that is, sc^3/sc^3 *tra/tra* did not survive.

Eosin (w^e) is paler and more yellowish in males than in females (BRIDGES and BREHME 1944), and facet (*fa*) is more extreme in males than in females (BRIDGES and BREHME 1944). In both these cases it is known that the normal sexual dimorphism is not due to the presence of a Y in the males and its absence in the females. In both these mutant types, the XX *tra/tra* individuals resembled their XX tra^+/tra sisters, and differed distinctly from their XY brothers.

In all three tested instances, therefore, the XX *tra/tra* individuals were like the females rather than the males with respect to sexual dimorphism dependent on mutant genotypes—though they were like males rather than females in the sexual characters (other than size and development rate) in which normal males and females differ.

One other similar test was carried out, with the semi-dominant sex-linked gene Bar (*B*). *B/B* and *B/+* in XX *tra/tra* closely resemble the same two types in their sisters.

It may be argued that the transformed individuals are better described as intersexes, rather than as males. I have preferred to call them males simply because they are indistinguishable from males in ordinary experiments—unless one dissects out their testes, and even the testes show no female characteristics. Perhaps the best reason for considering them intersexes is the short

sex-combs found on the single transformed superfemale that was seen. In any case, the gene is more extreme in its shifting of the sex of the individual than is any other yet described in any Drosophila. Only that recorded by LEBEDEFF (1934) for *D. virilis* was shown to be due to a gene in element D. The specimens here described resemble the most extreme types recorded by LEBEDEFF, but the extreme variability that he observed is here absent. It remains doubtful whether or not the genes in the two species represent corresponding loci. The present gene is certainly different from the one previously described intersex gene in *D. melanogaster*, since that lies in the second chromosome (L. V. MORGAN, in MORGAN, REDFIELD, and MORGAN 1943).

A mutant type of this sort, if the gene is autosomal, may easily be overlooked. It will give a sex ratio of 3 ♀ : 5 ♂ if both parents are heterozygous, but this will be difficult to distinguish from 1 : 1. The mating of heterozygous female × homozygous male gives 1 ♀ : 3 ♂, but this mating will be less likely to occur. The most likely situation for its detection will be that which actually led to the discovery of this one—namely, the presence of males of classes, with respect to sex-linked genes, that appear impossible from the known parentage. In those species where element D is part of X, detection through the distortion of the sex ratio should be easier.

SUMMARY

A recessive gene, *tra*, lying between 44.0 and 45.3 in the third chromosome of *Drosophila melanogaster*, transforms diploid females into sterile males.

The gene is without effect on males (that is, on XY diploids).

A single specimen indicates that *tra/tra* superfemales are intersexual but strongly male-like.

No fertile triploids homozygous for *tra* were obtained.

The gene is without effect on the sexual dimorphism of the mutant types scute-3, eosin, and facet—in all three of these cases the XX *tra/tra* specimens resemble normal females, rather than normal males, in the manifestation of the mutant phenotypes.

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SUMMARIES FROM FORTHCOMING PAPERS

RICK, CHARLES M. *A survey of cytogenetic causes of unfruitfulness in the tomato.*—Received January 18, 1945.—Gametic sterility is largely responsible for the unfruitfulness of 66 plants discovered in approximately 55,000 field plants of three tomato varieties. Failure of normal gamete formation was resolved to a cytogenetic basis in every case investigated.

Of the 66 unfruitful plants, 45 are triploid, 14 diploid, three tetraploid, two trisomic, and two haploid. Tetraploids are the most fruitful of the heteroploid plants, reflecting greater chromosome balance in gamete formation than in the other types. The majority of heteroploid plants are not found as members of multiple seedlings at germination.

The 14 diploids consist of the following:

Three plants aberrant in gross morphology. Sterility of these is probably conditioned either by a pleiotropic effect of the gene determining the deformity or by the deficiency of a chromosomal segment which includes a gene affecting the morphological character and another affecting sterility.

Three plants exhibiting male sterility, in each case determined by a single recessive gene.

Five plants normal in every respect except for complete pollen and ovule sterility. Failure of viable gamete formation in one plant results from asynaptic meiosis.

Three diploids lost during the investigation.

Gene mutation in the broad sense is probably responsible for the sterility of the 11 investigated diploid plants, for reasons discussed in the text. A gametic mutation rate of approximately 0.02 per cent was estimated from these findings.

The three tomato varieties are very similar in the frequency of all unfruitful types and in the proportions of each type. The relative proportions of the discovered types of cytogenetically conditioned sterility in the three varieties investigated here and in other varieties studied to a lesser extent are considered to be representative of most horticultural varieties of the tomato and perhaps of the species as a whole.

IRWIN, M. R., and R. W. CUMLEY. *Suggestive evidence for duplicate genes in a species hybrid in doves.*—Received January 22 1945.—The "hybrid substance" of the species hybrids between Pearlneck and Ring dove has been divided into three components by virtue of results obtained by agglutinin-absorption with the cells of various backcross hybrids. One of these fractions has been found always associated with the d-4 antigenic character of Pearlneck, another with the d-11. A third fraction detectable to date only with reagents prepared from a strongly reacting hybrid antiserum seemed to be linked but not completely, with each of several antigens of Pearlneck. This fraction appeared to be but one substance, or a group of very closely related substances, irrespective of association with different antigens of Pearlneck,

these later presumably being genetically as well as immunologically independent. These results suggest that genes with duplicate effects in interaction are located on several chromosomes of Pearlneck.

There is still another possible, but perhaps less probable, explanation of the association of the third fraction of the hybrid substance with several of the unit antigens of Pearlneck. In this explanation, it would be assumed that this fraction was produced by a gene or genes on but one chromosome of Pearlneck interacting in the species hybrid with one or more genes from Ring dove, and the seeming association with various antigens specific to Pearlneck was then entirely one of chance.

LANDAUER, WALTER. *Recessive rumplessness of fowl with kypho-scoliosis and supernumerary ribs.*—Received January 27, 1945.—A new skeletal mutation of fowl was described which has the following principal morphological features.

The pygostyle and the free caudal vertebrae may be entirely absent; more commonly they are rudimentary and fused together into a bony knob. According to the degree of abnormality of the caudal skeleton, the uropygial gland and the tail feathers may be lacking, or the gland may be rudimentary, and there may be a reduced number of drooping tail feathers.

The intermediate conditions lead by imperceptible steps from complete rumplessness to an entirely normal tail. In all the preceding peculiarities the new mutation resembles closely the forms of expression of the dominant rumpless mutation and its modifications.

The following morphological traits distinguish the new mutation from dominant rumplessness. The rudimentary caudal vertebrae frequently have the appearance of lateral compression and show marked lordosis. In many animals there is a synsacral kypho-scoliosis of varying degree, with a compensatory thoracic or synsacro-thoracic scoliosis in the opposite direction. The pelvic bones of such animals are deformed. The acetabula stand at different levels, and this asymmetry is corrected, as far as locomotion is concerned, by coxa vara of the femur with the lower articulation. A less common part of the syndrome is the occurrence of supernumerary ribs, posterior to the last normal pair. These supernumerary ribs may be unilateral or bilateral, rudimentary or fully formed.

Sex acts as a modifier of this mutation. In males the various features of the whole syndrome tend to find more frequent and more severe expression.

The mutation is completely recessive to the normal condition. It was found in White Leghorn stock. It appears that the expression of the mutation is influenced by the action of a series of modifying genes and that the latter account for the low degree of "penetrance" and "expressivity." Some of the genetic modifiers may be sex-linked, but others and the main gene are autosomal.

Completely rumpless embryos have a slightly reduced chance of hatching; otherwise the mutation does not exert a marked effect on embryo survival. During the postnatal growth period there is a somewhat increased mortality

of chicks with an abnormal caudal skeleton as compared with their sibs with normal tail vertebrae.

The ash and calcium content of the pelvic bones is reduced in all adult animals of the recessive rumpless stock, including those with normal tail vertebrae. Percentage of water in these bones is increased at the expense of organic material. This hydration is found also in the femur and tibia of rumpless and intermediate rumpless animals from the recessive rumpless stock, but not in those birds which have a normal caudal skeleton. Chemical analysis did not reveal changes of composition in the bones of newly-hatched chicks, but by alizarin staining, delayed calcification could be demonstrated in the synsacral vertebrae, the pelvis and the uncinate processes of the ribs.

There are no signs of rickets (vitamin D deficiency), but changes in chemical composition of the axial skeleton probably account for reduced mechanical strength (lowered resistance to normal stresses), resulting in kypho-scoliosis.

There is considerable evidence that the modifiers of rumplessness are genes which serve as stabilizers of normal development of the caudal skeleton.

COOPER, D. C., and R. A. BRINK. *Seed collapse following matings between diploid and tetrapolid races of Lycopersicon pimpinellifolium.*—Received January 27, 1945.—A comparative histological study of seed development following reciprocal matings between diploid and tetraploid strains of *Lycopersicon pimpinellifolium* and crosses of these races with *L. peruvianum* is reported.

A high percentage of the flowers pollinated formed mature fruits in all matings except 2n×4n. The flowers and young fruits in the latter case were shed within eight days. The initial set was high in the 4n×4n mating, but numerous immature fruits were shed at intervals up to 24 days.

Practically all the seeds formed following the 2n×2n mating were plump at maturity. About two-thirds of those found in the 4n×4n fruits were sound, and the remainder shrivelled. The 4n×*L. peruvianum* cross likewise gave a relatively high proportion of plump, although small, seeds. The seeds in the mature fruits resulting from the 4n×2n and 2n×*L. peruvianum* matings, on the other hand, were much shrunken and incapable of germination.

Double fertilization takes place, and both endosperm and embryo start growth in all developing seeds. Fertilization was found to occur approximately 24 hours following pollination of 2n flowers but is somewhat delayed in the 4n flowers regardless of the type of mating.

The endosperm develops rapidly in the 2n×2n and 4n×4n seeds and differentiates early, the peripheral layer of cells acting as an absorbing tissue. The endothelium—that is, the inner layer of cells of the expanding integument adjacent to the endosperm—remains a single layer of densely cytoplasmic cells in the growing seed. Several layers of cells of the integument immediately outside the endothelium become empty of their contents during the early stages of development of the endosperm, thus serving as a source of nutrients.

The chalazal aperture opposite the end of the vascular bundle in conjunction with the endothelium serves as a pathway for nutrients at later stages of development of the endosperm.

The embryo grows at the expense of the endosperm.

The development of the 4n×*L. peruvianum* seed is essentially similar although much slower than that of the 4n×4n seed.

Growth of the endosperm in the 2n×4n, 2n×*L. peruvianum* and 4n×2n seeds is slow, and the cells at the chalazal end are large and highly vacuolated at 144 hours. By this time there is a conspicuous thickening of the endothelium mainly on the dorsal side of the endosperm. Shortly thereafter the endothelium becomes actively meristematic and grows rapidly so that this tissue has within a few days completely filled the space formerly occupied by the endosperm.

A large amount of deeply-staining material accumulates in the cells of the chalazal pocket during the course of collapse of the aborting endosperms.

The embryo grows slowly and is very small and starved in appearance by the time it has become completely surrounded by the hyperplastic endothelium. Shortly thereafter the embryo dies, and a much-shrivelled seed is found in the mature fruit.

The course of seed failure associated with matings between the diploid and its autotetraploid is very similar to that found following the interspecific cross.

PATTERSON, J. T., and TH. DOBZHANSKY. *Incipient reproductive isolation between two subspecies of Drosophila pallidipennis.*—Received February 14, 1945.—*Drosophila pallidipennis pallidipennis* and *D. pallidipennis centralis* are known to occur in southern Brazil and in Mexico, respectively. The strains examined show slight morphological differences sufficient to distinguish the subspecies in the living material raised under standardized conditions but probably not in dried specimens raised in different environments.

The gene arrangements in the chromosomes of the two subspecies are identical, except for an inversion in one of the autosomes. The pairing of the homologous chromosomes in the salivary gland cells of the hybrids is as intimate as it is in the parental forms. The subspecies cross readily and produce fully viable hybrids. No sexual isolation is apparent. The F_1 hybrid males are completely sterile, but the females are fertile. Females obtained in the offspring of the backcross are fertile. Already some of the males obtained in the first backcross are fertile, and the proportion of fertile males increases in the offspring of the second backcross. Taken as a whole, the data suggest that the sterility of the hybrids is caused by interaction of several, perhaps of many, genes contributed by the parental forms. Gross disturbances are apparent in the spermatogenesis of the sterile hybrid males, although the meiotic chromosome pairing seems to be normal.

The combination of a slight but perceptible morphological differentiation with the near-identity of the gene arrangements, and of the lack of sexual isolation with hybrid sterility suggests that the different components of the process of speciation characteristic for the genus Drosophila are largely independent.

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Edited by

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